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A PHYLOGENETIC REVISION OF THE PHALLOSTETHID FISHES
(ATHERINOMORPHA, PHALLOSTETHIDAE)

By

Lynne R. Parenti

California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118

ABSTRACT: The Phallostethidae (including Neostethidae) comprises a group of small to minute atherinomorphic fishes distinguished from all other teleosts by the presence in males of a complex, bilaterally asymmetric, subcephalic copulatory organ, the priapium. I recognize 19 species in four genera: *Phallostethus* Regan, 1913, *Neostethus* Regan, 1916, *Gulaphallus* Herre, 1925, and *Phenacostethus* Myers, 1928. This includes one new species, *Neostethus robertsi*, from Luzon. Phallostethids are widely distributed throughout coastal brackish waters from Thailand, Singapore, Malaysia, and the Philippines, as well as inland freshwater streams of Luzon and Borneo.

The three objectives of this review are to: (1) describe the anatomy and variation of the priapium and propose synonymy and probable homology of its many and varied osteological and myological modifications; (2) present taxonomic synonymies and diagnoses of the 19 species in four genera; and (3) hypothesize phylogenetic relationships among the species by grouping into higher categories based primarily on the presence of shared derived characters of the priapium.

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INTRODUCTION

Regan (1913) named the first known phallostethid species *Phallostethus dunckeri* in honor of Georg Duncker (1904), who first reported this unusual group of fishes from Johore on the Malay Peninsula. During the following three decades, attention focused on description of new species and genera (e.g., Regan 1916; Herre 1925, 1926; Myers 1928; Villadolid and Manacop 1935; Manacop 1936), anatomy of the complex copulatory organ, the priapium (e.g., Bailey 1936; Aurich 1937; TeWinkel 1939; Woltereck 1942a, b), and consideration of the relationships of phallostethids to other fishes (e.g., Smith 1927; Myers 1935; Hubbs 1944).

Presence of a priapium led to speculation that phallostethids must be live bearers (e.g., Regan 1913). However, Smith (1927) observed female phallostethids in Thailand depositing eggs. Villadolid and Manacop (1935) confirmed that females of *Gulaphallus mirabilis* lay fertilized eggs following copulation. Structure of ovaries and testes, presence of sperm bundles (spermato-

zeugmata), and mode of internal fertilization are currently under investigation (Grier and Parenti, in prep.).

Early descriptions of phallostethids followed the convention of naming morphologically distinctive populations not just as new species but as new genera as well. In the last comprehensive review of phallostethids, Herre (1942) recognized 18 species classified in 10 genera, one of which had two subgenera (Table 1).

Interest in phallostethid systematics was renewed with description of a new species, *Phenacostethus posthon* Roberts, 1971a and a detailed osteological study of *Neostethus bicornis* Regan (formerly in *Ceratostethus*) (Roberts 1971b). Despite extensive work by Roberts, numerous questions remained concerning the relationships of phallostethids to other atherinomorphs, limits of, and relationships among, genera, and total number of recognizable species. It was with the goal of answering these questions that I began my studies of phallostethids.

A preliminary review resulted in detailed osteology of *Phallostethus dunckeri* and the proposal that phallostethids are the sister group of the Indo-Pacific atherinoid, *Dentatherina merckeri* Patten and Ivantsoff, 1983 (Parenti 1984). I described a new species, *Phenacostethus trewavasae* Parenti, 1986a and brought the total number of then recognized species to 20. Homology of priapial structures, always a challenge to students of phallostethids, was considered by examining development of the pelvic fins of one species, *Gulaphallus falcifer* Manacop (formerly in *Manacopus*), in which there are bilaterally asymmetric adult females as well as males (Parenti 1986b). I (Parenti 1986c) reviewed the association between bones and teeth in teleost fishes because in some phallostethid species there is a perichondrally ossified lower jaw bone, the paradentary, that may possess teeth.

Much of the information compiled on phallostethid fishes has been inaccessible to, or ignored by, systematists because of the array of peculiar names applied to parts of the complex priapium and because of the small size of phallostethids. Further, no previous classifications summarize cladistic relationships adequately; rather, they emphasize gross phenetic differences among species.

Phallostethid fishes are distributed throughout coastal mainland and insular Southeast Asia from Thailand to the Philippines (Fig. 1), entirely west

of Wallace's Line, one of several hypothetical boundaries separating the Asian from the Australian biota (see Whitmore 1987). Cladistic relationships of phallostethids can be used to present a working hypothesis of the distributional history of one segment of the Indo-Australian biota (see methodology in Humphries and Parenti 1986). Results from this study will be combined with those of other analyses to prepare a historical biogeographic analysis of the Indo-Australian atherinomorph fishes (Parenti, in prep.).

This review has three objectives: (1) to describe the anatomy and variation of the priapium and propose synonymy and probable homology of its numerous osteological and myological modifications; (2) to present taxonomic synonymies and diagnoses of the herein recognized 19 species, with one described as new, classified in four genera; and (3) to hypothesize relationships among the species, grouping them into higher categories, primarily on synapomorphies of the priapium.

MATERIALS AND METHODS

I observed osteological characters on specimens counterstained with alcian blue and alizarin red S (Dingerkus and Uhler 1977) or stained solely with alizarin. I examined specimens with a Zeiss SV8 dissecting microscope and recorded data using a drawing tube and photomicrography attachments. Representatives of 18 of the 19 currently recognized phallostethid species were examined as part of my recent studies. No specimens of *Neostethus ctenophorus* (Aurich, 1937) were available; characters are from the original description.

Meristic data (except for scale counts) were tabulated from cleared and stained specimens. In recording meristic data (Table 2), the terminal half-centrum is counted as one vertebra, and all fin spines and rays are counted, including, for example, the last two anal rays which articulate with just one pterygiophore.

Institutional abbreviations follow the Standard Symbolic Codes for Institutional Research Collections in Herpetology and Ichthyology (Leviton et al. 1985). The following abbreviations are defined: Dist., district; Is., island; Prov., province; R., river; and SL, standard length. Catalog numbers for phallostethid material examined are given in the text.

TABLE 1. Comparison of Herre's (1942) classification of Phallostethids with that presented herein.

Herre (1942)	Present paper
<i>Phallostethus dunckeri</i>	<i>Phallostethus dunckeri</i>
<i>Phenacostethus smithi</i>	<i>Phenacostethus smithi</i>
	<i>Phenacostethus posthon</i>
	<i>Phenacostethus trewavasae</i>
<i>Mirophallus bikolanus</i>	<i>Gulaphallus bikolanus</i>
<i>Solenophallus thessa</i>	<i>Neostethus thessa</i>
<i>Gulaphallus eximius</i>	<i>Gulaphallus eximius</i>
<i>Gulaphallus mirabilis</i>	<i>Gulaphallus mirabilis</i>
<i>Ceratostethus bicornis</i>	<i>Neostethus bicornis</i>
<i>Manacopus falcifer</i>	<i>Gulaphallus falcifer</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>amaricola</i>	<i>Neostethus amaricola</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>lankesteri</i>	<i>Neostethus lankesteri</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>siamensis</i>	synonym of <i>Neostethus lankesteri</i>
<i>Neostethus</i> (<i>Neostethus</i>) <i>villadolidi</i>	<i>Neostethus villadolidi</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>borneensis</i>	<i>Neostethus borneensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>coronensis</i>	synonym of <i>Neostethus borneensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>panayensis</i>	<i>Gulaphallus panayensis</i>
<i>Neostethus</i> (<i>Sandakanus</i>) <i>zamboangae</i>	<i>Neostethus zamboangae</i>
	<i>Neostethus robertsi</i>
<i>Ctenophallus ctenophorus</i>	<i>Neostethus ctenophorus</i>
<i>Plectrostethus palawanensis</i>	<i>Neostethus palawanensis</i>

The theory of phylogenetic reconstruction followed is that commonly referred to as phylogenetic systematics or cladistics, as outlined by Hennig (1966) and modified by numerous authors (see review by Wiley 1981). Genera and other higher taxa are defined as monophyletic by the sharing of homologous derived characters, termed synapomorphies. Species are defined as the smallest, recognizable, morphologically distinctive groups of males and females which may share homologous derived characters, termed autapomorphies.

For priapial characters, a state that is unique to a particular phallostethid species, or group of species, is treated as derived. This is a special case of the method of outgroup comparison (see Maddison et al. 1984) which is used to determine polarity of non-priapial characters. The following atherinomorph specimens were examined for outgroup comparison: *Bedotia* sp., aquarium material, CAS 44367 (1 of 3 counterstained); *Dentatherina merceri*, Moluccas, USNM 230374

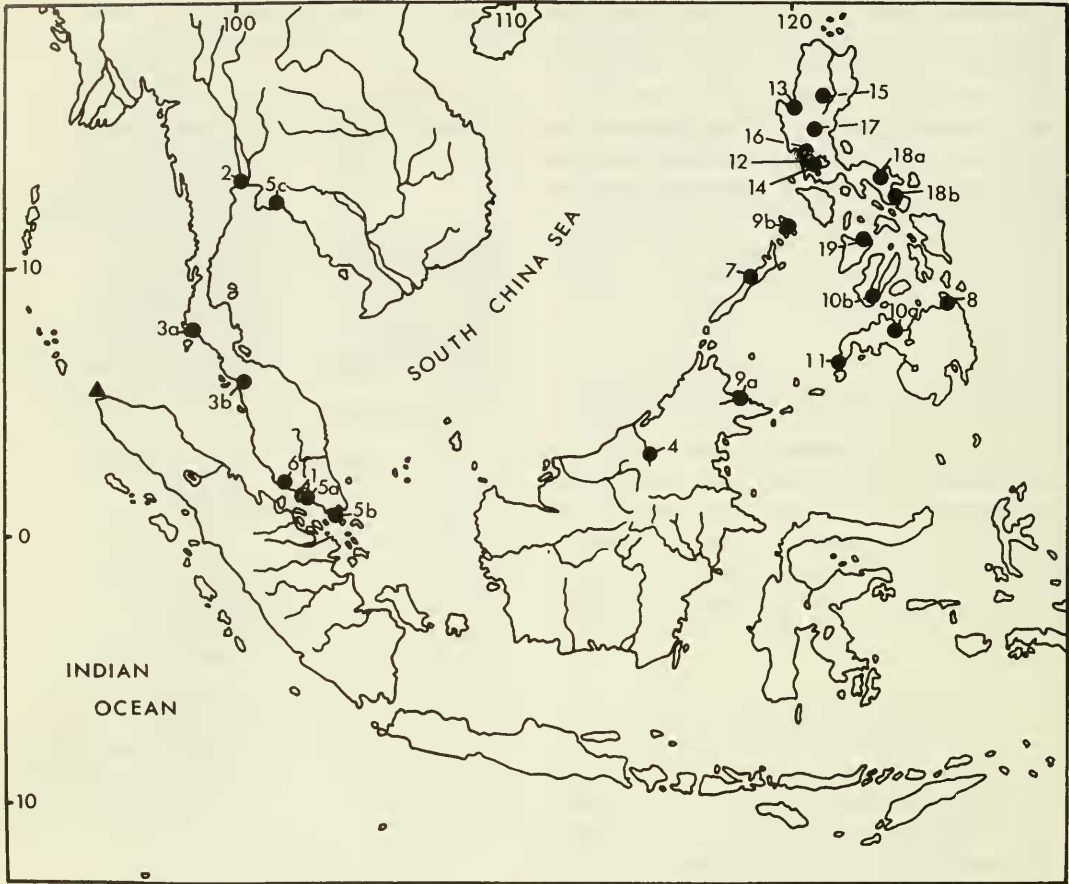


FIGURE 1. Distribution of phallostethids. Solid circles, type localities of the 19 currently recognized phallostethid species: 1. *Phallostethus dunckeri* Regan, Muar R.; 2. *Phenacostethus smithi* Myers, Bangkok; 3. *Phenacostethus posthon* Roberts, a. Khlong Kla Sohm, b. Khlong Langu; 4. *Phenacostethus trewasae* Parenti, Baram R.; 5. *Neostethus lankesteri* Regan, a. Muar R., b. Singapore, c. Chantabun R.; 6. *Neostethus bicornis* Regan, Kuala Langat; 7. *Neostethus palawanensis* (Myers), Ulugan Bay; 8. *Neostethus thessa* (Aurich), Lake Mainit; 9. *Neostethus borneensis* Herre, a. Sandakan Bay, b. Coron; 10. *Neostethus villadolidi* Herre, a. Misamis, b. Dumaguete; 11. *Neostethus zamboangae* Herre, Zamboanga; 12. *Neostethus amaricola* (Villadolid and Manacop), Pasay; 13. *Neostethus robertsi*, new species, Calasiao R.; 14. *Neostethus ctenophorus* (Aurich), Laguna de Bay; 15. *Gulaphallus eximius* Herre, Nueva Vizcaya; 16. *Gulaphallus mirabilis* Herre, Ibo R.; 17. *Gulaphallus falcifer* Manacop, Pampanga and Nueva Ecija; 18. *Gulaphallus bikolanus* (Herre), lakes Bato and Lanigay; and 19. *Gulaphallus panayensis* (Herre), Panay. Solid triangle, unsubstantiated report of unidentified phallostethid from off northwestern Sumatra by Aurich (1937).

(2 of 42 counterstained); *Hypoatherina ovalaia*, Vanuatu, Malekula Is., CAS 62564 (2 of 10 counterstained); *Melanotaenia affinis*, northern New Guinea, CAS 40573 (4 of 31 counterstained), and *Pseudomugil signifer*, New South Wales, Australia, CAS 62565 (6 of 62 counterstained).

The pattern of reduction or loss of a character, which is common in atherinomorphs, is useful as a source of information for phylogenetic reconstruction when correlated with other, more

complex characters (Parenti 1986b). Ontogenetic data are used to infer homology among character states (Patterson 1982) and as an additional source of information for character polarity (Nelson 1978). Ontogenetic transformation and pattern of reduction or loss are the most reliable sources of information on polarity of states of the priapium. Outgroup comparison is limited because a priapium is not found, even in a simplified condition, outside the Phallostethidae.

TABLE 2. Meristic characters of phallostethids. D1 = first dorsal rays, D2 = second dorsal rays, A = anal rays, P1 = pectoral rays, BR = branchiostegal rays, V = vertebrae, SLS = scales in lateral series.

Species	D1	D2	A	P1	BR	V	SLS
<i>N. lankesteri</i>	2	6-7	16-17	11-12	5	34-35	31-32
<i>N. bicornis</i>	1	5-6	15-16	10-11	5-6	36-37	31-34
<i>N. palawanensis</i>	1	5-6	15-16	11	5	34-35	30-32
<i>N. thessa</i>	0	8-10	17-22	12-13	5	36-37	32-34
<i>N. borneensis</i>	1-2	5-6	13-16	10-12	5	31-32	25-27
<i>N. robertsi</i>	2	6	17-18	10-11	5	36	30
<i>N. villadolidi</i>	2	5-6	14-16	9	5-6	35-36	30-32
<i>N. zamboangae</i>	2	5-6	15-17	9	5-6	35-36	29-32
<i>N. amaricola</i>	1-2	5-6	16	10-11	5-6	35-36	32
<i>N. ctenophorus</i> ^a	2	5-7	14-17	10-11	—	—	31-33
<i>G. eximius</i>	1-2	7-8	15-18	11	5	36-37	52-58
<i>G. mirabilis</i>	1-2	7	17-18	10-12	5	36-37	36-38
<i>G. falcifer</i>	1-2	8	17	10	5	35	32
<i>G. bikolanus</i>	0	6	14-17	11-13	5	35-36	32
<i>G. panayensis</i>	1-2	6-7	13-15	11	5	31-33	28-30
<i>P. dunckeri</i>	0	8-10	26-28	9-10	4	40	^b
<i>P. trewavasae</i>	1	6	14-15	9-10	5	34	^b
<i>P. posthon</i>	1	5-6	14-15	9-10	4	34-35	^b
<i>P. smithi</i>	1	6-7	14-15	9-10	4-5	33-35	^b

^a From Aurich (1937).

^b Because Phallostethini scales are small and deciduous, it is difficult to record an accurate count.

RELATIONSHIPS OF PHALLOSTETHIDS TO
OTHER ATHERINOMORPHS

None has questioned monophyly of the phallostethids, i.e., all phallostethid males have a priapium, and none has argued that the priapium is not a uniquely evolved structure. I present no argument here to contradict phallostethid monophyly. However, I acknowledge that information from some future study could lead us to conclude that not all priapia are homologous.

Perhaps the only currently controversial aspect of phallostethid systematics is their relationship to other acanthopterygian fishes. The following four issues, with references for arguments pro and con, summarize the debate:

1. Atherinomorphs are monophyletic, although their relationship to other acanthomorph teleosts remains obscure (Rosen 1964; Rosen and Parenti 1981; Collette et al. 1984; Parenti 1981, 1984; Grier and Collette 1987).

Since Rosen (1964) formally recognized the series Atherinomorpha, which comprises the atherinoids, cyprinodontiforms, and beloni-forms, the group has been accepted by ichthyologists, although with some reservation (e.g., Roberts 1971b). However, it is generally agreed that systematic differences between the Ather-

inidae and Cyprinodontidae are not as great as had been thought by Hubbs (1944). Traditional groups such as the Percesoces—which contains the mullets (Mugiloidea), polynemids (Polynemoidea), and phallostethids (Phallostethoidea), according to the classification of Myers (1937)—are no longer recognized. However, possible atherinomorph relatives may be among constituents of these taxa, such as the mugilids. Confirmation of the sister group of the Atherinomorpha, as well as other acanthomorph taxa, is the subject of ongoing studies by numerous systematic ichthyologists, including myself, and will not be discussed further here.

2. Phallostethids are atherinomorphs (Rosen and Parenti 1981; Parenti 1984; White et al. 1984; Ivantsoff et al. 1987), or may be related to polynemids (Bailey 1936) or to gobioids (Springer 1983).

Determining whether phallostethids are atherinomorphs requires a well-corroborated definition of the series Atherinomorpha; phallostethids either fit the definition or they do not. Rosen and Parenti (1981) listed defining characters of the Atherinomorpha, which includes a derived ethmoid region and hyobranchial apparatus. Recent workers have corroborated the

proposal that the Atherinomorpha is monophyletic (e.g., Grier and Collette 1987), and that phallostethids are atherinomorphs (Parenti 1984; Ivantsoff et al. 1987).

Bailey (1936) hypothesized a close relationship between phallostethids and polynemids based on the shared close association of the pelvic and pectoral girdles. Springer (1983) cited shared reductions between phallostethids and gobioids to suggest, in a footnote, their possible close relationship. To endorse the hypothesis that phallostethids are atherinomorphs requires that the characters shared by phallostethids and polynemids or gobioids be treated as convergent. However, Springer's (1983) proposal expands the list of possible atherinomorph close relatives to polynemids, mullets, and gobioids.

3. Atherinoids, including the silversides (or hardyheads), rainbowfishes, and phallostethids, are not monophyletic (Rosen and Parenti 1981; Parenti 1984; Ivantsoff et al. 1987) or atherinoids are monophyletic (White et al. 1984).

Rosen and Parenti (1981) and Parenti (1984) proposed that atherinoids do not constitute a monophyletic group because they exhibit transformation series for certain characters, such as transformation of the first dorsal fin from plesiomorphic atherinoids (e.g., *Bedotia* and *Melanotaenia*) in which it is well developed, to phallostethids in which it is reduced or absent. This view was supported by Ivantsoff et al. (1987). White et al. (1984) proposed two developmental characters to support their view that atherinoids are monophyletic. This issue will be clarified when there is a well-corroborated proposal of relationships among the major groups of atherinomorph fishes, a study under progress.

4. Phallostethids are the sister group of *Dentatherina* Patten and Ivantsoff, 1983 (Parenti 1984), or the close relationship of phallostethids to *Dentatherina* is not supported (Ivantsoff et al. 1987).

Parenti (1984) proposed a close relationship between *Dentatherina mercuri* and phallostethids based on, among other characters, presence of a paradentary bone. At issue is whether the paradentary elements—ossifications of the labial ligament—are homologous in phallostethids and *Dentatherina*. The phallostethid paradentary bone is composed of acellular bone surrounding hyaline cartilage (Parenti 1986c; Ivantsoff et al. 1987). The *Dentatherina* paradentary bone is

composed of hyaline cartilage with a calcified core (Ivantsoff et al. 1987).

Ivantsoff et al. (1987) cited the histological differences between the phallostethid and *Dentatherina* paradentary elements to conclude that the bones are not homologs and, therefore, cannot be used to propose a close relationship between two taxa. They also rejected homology based on the conclusion that calcification or ossification in a labial ligament could result as a response to stress. I concur that if the bones are not homologous they cannot be used to propose a close relationship between two taxa. However, I reject the functional argument against homology. The labial ligament could become calcified or ossified in any taxon in which it occurs; within atherinomorphs, it is reported ossified only in phallostethids and *Dentatherina*. In my opinion, additional characters are needed to accept or refute the proposal of a phallostethid–*Dentatherina* sister group.

Phallostethids need no additional support to be accepted as a monophyletic group; a seemingly endless number of derived characters could be listed to define them (see Synonymy and Homology of Priapial Structures). Further research should focus on the question: to which group of Old World atherinoids are phallostethids most closely related? Hubbs (1944:70) summarized the importance of this type of question in systematics: "Whether or not a suborder or an order be recognized for the Phallostethidae, on the basis of the bizarre copulatory organ (the priapium) and of other structures, is, like most questions of ranking, of no great inherent significance. Whether the relationship of the family is with Cyprinodontidae or with the Atherinidae, or with neither, is a problem of greater meaning."

SYNONYMY AND HOMOLOGY OF PRIAPIAL STRUCTURES

Since Regan (1913) first described the complex anatomy of the phallostethid priapium, students of this unusual group of fishes have struggled to attain a stable, appropriate set of terms for the numerous priapial structures (Regan 1916; Bailey 1936; Aurich 1937). Nearly every paper discussing priapial anatomy contains errors of identification or proposed homology. A common mistake is to refer to the same structure by more than one name in a single paper.

Proliferation of names for priapial structures was encouraged by Regan (1916), who believed that the priapium was a new morphological structure with no known homolog among teleost fishes. For example, Regan gave the adjectival name "anterior infrasulcar" to a bone which I consider the homolog of one of the pelvic bones.

No doubt, a stable nomenclature has not been attained because homology of the priapial structures has not been well understood, and because structure of the priapium may vary greatly from one phallostethid genus to another. Bailey (1936) concluded that priapia of *Phenacostethus smithi* and *Gulaphallus mirabilis*, and hence of all phallostethids, correspond bone-for-bone. Furthermore, he believed that these structures could be identified in polynemids, close relatives of phallostethids according to Bailey. However, he did not examine a species of *Neostethus*, which has bony elements not found in either *Phenacostethus* or *Gulaphallus*. Also, a close relationship between polynemids and phallostethids has not been supported (see Relationships of Phallostethids to other Atherinomorphs).

The priapium may be thought of as having three structural and functional components: suspensory, holding or clasping, and papillary (Bailey 1936). The suspensory component consists of expanded anterior pleural ribs, including anteriorly expanded cleithra in *Neostethus* and *Gulaphallus*, as well as modified pelvic bones. The holding or clasping component consists of the externalized ctenactinia and/or toxactinium, the movement of which is controlled mainly by a set of longitudinal muscles. The papillary component consists of the seminal and infrasulcar papillae and papillary bones used in the transfer of sperm bundles from males to females.

To describe the diverse and detailed priapia of phallostethids, I have compiled a synonymy of priapial structures (Table 3 and below). In addition, I propose, where possible, the homolog of each element as found in relatively unmodified atherinoid fishes. Listed is the name of a structure, first and subsequent citations, including misidentifications, in major papers on phallostethids, brief description, probable homolog, known synonyms, and citations.

antepleural cartilage or bone (Figs. 2, 3)—Regan (1916:7), Roberts (1971b:408), Parenti (1986a:228). A large block of cartilage, sometimes par-

tially or fully ossified, that lies anterior to the distal tips of the first pleural ribs in males.

aproctal side or aspect—Regan (1913:552, 1916:5), Herre (1942:138), Parenti (1986a:225). That side of the male's body without the anal opening. Male phallostethids are bilaterally asymmetric such that the anus and seminal papilla are offset to opposite sides of the body (see Parenti 1986a).

axial bone—Regan (1916:7), Bailey (1936:464), TeWinkel (1939:61), Villadolid and Manacop (1935:215). An elongate bone with rodlike spine and broad, dorsal crest. The aproctal and proctal axial bones are homologous with the pelvic bones (Regan 1913, 1916; Bailey 1936).

aproctal axial bone (Figs. 2–5)—Roberts (1971b:408–409). The axial bone on the aproctal side of the body. Synonyms: anterior infrasulcar bone (Regan 1916:8, Bailey 1936:466), desmactinium (Aurich 1937:267), ctenactinium (misidentification, Herre 1925:508, 1926:539; Myers 1937:142), second ctenactinium (misidentification, Bailey 1936:463), short ctenactinium (misidentification, Villadolid and Manacop 1935:195).

proctal axial bone (Figs. 3–5)—Roberts (1971b:408–409). The axial bone on the proctal side of the body, with which the toxactinium and ctenactinia articulate. Synonym: axial bone (Regan 1916:7; Myers 1935:5; Bailey 1936:464; Parenti 1986a:228, 1986b:308).

ctenactinium—Regan (1913:552, 1916:5), Myers (1928:1, 1935:5), Bailey (1936:465–466), Manacop (1936:376), Aurich (1937:264), TeWinkel (1939:62), Herre (1939:140, 1942:138), Wolterreck (1942b:339), Roberts (1971a:6, 1971b:393), Parenti (1984:6, 1986b:309). One of two curved, rodlike priapial bones that articulate with the posterior end of the proctal axial bone. Homologous with a pelvic fin ray (Bailey 1936).

first ctenactinium (Figs. 3–5)—The prominent, elongate externalized priapial bone in *Neostethus* and *Gulaphallus*. Usually called the ctenactinium, referred to herein as the first ctenactinium to distinguish it unambiguously from the second ctenactinium. Synonym: toxactinium (misiden-

TABLE 3. Summary of names of priapial structures and synonyms. See text for definitions and references.

Priapial structure	Synonyms
antepleural cartilage or bone	
aproctal side or aspect	
axial bone	
aproctal axial bone	anterior infrasulcar bone, desmactinium, ctenactinium, second ctenactinium, short ctenactinium
proctal axial bone	axial bone
ctenactinium	
first ctenactinium	toxactinium
second ctenactinium	Priapklaue, "pulvinular spine," anterior infrasulcar bone
efferent groove	
epididymis	
fringe	terminal coil of vas deferens
	comblike projections, comblike cilia, cilia, comb
glandular groove	
infrasulcar bones	
anterior infrasulcar bone	aproctal axial bone
posterior infrasulcar bone	
infrasulcar prominence or papilla	
keel	embryonic fin-fold, fringe
longitudinal muscles	
ctenactinial muscle	
outer muscle of aproctal side	
inner muscle of proctal side	
muscle of proctal side	
papillary bones	penial bones
penial bone	
basipenial bone	
papillary bone	
prepapillary bone	
cristate bone	
pleuro-priapial muscle	
priapial process of cleithra	
priapial ribs	first pleural ribs
aproctal priapial rib	first pleural rib on aproctal side
proctal priapial rib	first pleural rib on proctal side
priapium	
proctal side or aspect	
pulvinular appendage	
pulvinular spine	
pulvinular bones	
inner pulvinular bone	
outer pulvinular bone	toxactinium

TABLE 3. Continued.

Priapial structure	Synonyms
pulvinulus	shieldlike pad, pulvinular pad
seminal papilla	genital papilla, penis
toxactinium	outer pulvinular bone, pulvinular bone, toxactinial bone, inner pulvinular bone, modified pulvinulus
uncus	

 tificalion, Herre 1925:508, 1926:539; Villadolid and Manacop 1935:200).
 second ctenactinium (Figs. 2, 4, 5, 9)—The shorter of the two externalized priapial bones that may have serrations, as in *Phallostethus*, and *N. zamboangae*. Synonym: Priapklaue (Aurich 1937:267), "pulvinular spine" or tip of anterior infrasulcar bone (misidentification, Herre 1942:138).

efferent groove—Regan (1916:5). A groove on the aproctal side of the body, posterior to the glandular groove and separated from it by the seminal papilla and infrasulcar prominence or papilla.

epididymis (Fig. 5)—Regan (1913:555), Roberts (1971a:6), Parenti (1986a:231). The coiled vas or ductus deferens enclosed in a membranous sac at posterior extent of the priapium. Synonym: terminal coil of vas deferens (Regan 1916:4).

fringe (Figs. 3, 13)—Regan (1916:5), Roberts (1971b:408). Posterior ends of pelvic fin rays that extend beyond the posteroventral outline of the epididymis. Synonyms: comblike projections (Myers 1928:8; Villadolid and Manacop 1935:197), comblike cilia (Herre 1939:140), cilia (Herre 1942:138), comb (Roberts 1971b:408).

glandular groove—Regan (1916:5). A groove on the aproctal side of the body at the boundary between the priapium proper and the body wall.

infrasulcar bones—Regan (1916:8). Two bones, referred to by Regan (1916) as the anterior and posterior infrasulcar, that, in part, support the infrasulcar and seminal papillae.

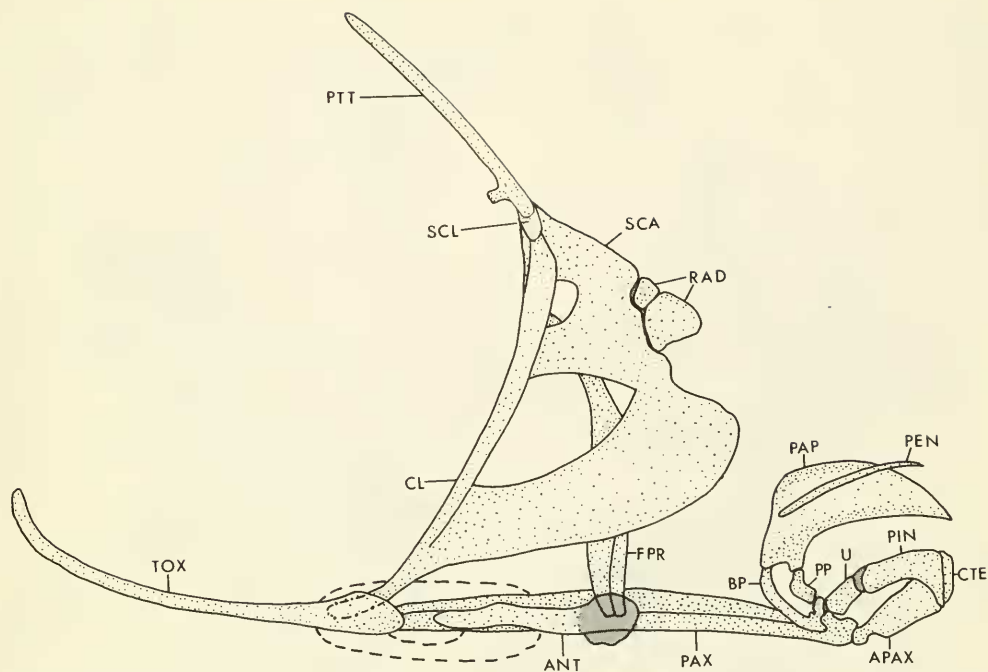


FIGURE 2. Diagrammatic representation of modified pelvic and pectoral fins in the priapium of a dextral male, *Phenacostethus smithi* (CAS-SU 35957 and modified in part from Bailey 1936), slightly exploded view from proctal side. Anterior to left. Dashed line, outline of pulvinulus; dotted and dashed line, anterior extent of cleithrum. Dense stippling, cartilage; light stippling, bone. Abbreviations: ant, antepleural bone and cartilage; apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; cte, second ctenactinium; fpr, first pleural ribs; pap, papillary bone; pax, proctal axial bone; pen, penial bone; pin, posterior infrasulcar bone; pp, prepapillary bone; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum; u, uncus.

anterior infrasulcar bone—Regan (1916:8).
See aproctal axial bone.

posterior infrasulcar bone (Fig. 2)—Regan (1916:8), Bailey (1936:467). A rod-shaped bone at the base of the aproctal axial bone with a laminar projection that lies ventral to the aproctal axial bone, reaching the base of the infrasulcar papilla or prominence.

infrasulcar prominence or papilla—Regan (1916: 5, 8), Herre (1939:141). A papilliform projection anterior to the seminal papilla, supported internally by a posterior projection of the aproctal axial bone.

keel—Regan (1913:550), Myers (1935:5), Roberts (1971b:410). A median, abdominal, slightly frayed, fleshy ridge between the urogenital opening and anterior rays of the anal fin. Homologous with embryonic fin-fold (Roberts 1971b). Synonym: fringe (alternate

term not homologous with fringe as defined above, Regan 1916:2; Myers 1928:5).

longitudinal muscles (Fig. 6)—Regan (1916:13, fig. 10; 1916:14). Four fusiform muscles—ctenactinial muscle, outer muscle of the aproctal side, inner muscle of the aproctal side, and muscle of the proctal side—that originate on the axial bones and control copulatory movements of the priapium. Precise homology with pelvic fin muscles (Winterbottom 1974) is unclear.

ctenactinial muscle (Fig. 6)—Regan (1916: 14). Largest of the longitudinal priapial muscles, with an origin at the anterior end of the dorsal crest of the aproctal axial bone and insertion at the proximal end of the ctenactinium.

outer muscle of the aproctal side (Fig. 6)—Regan (1916:14). An elongate muscle that originates on the concave, aproctal side of the main crest of the proctal axial bone

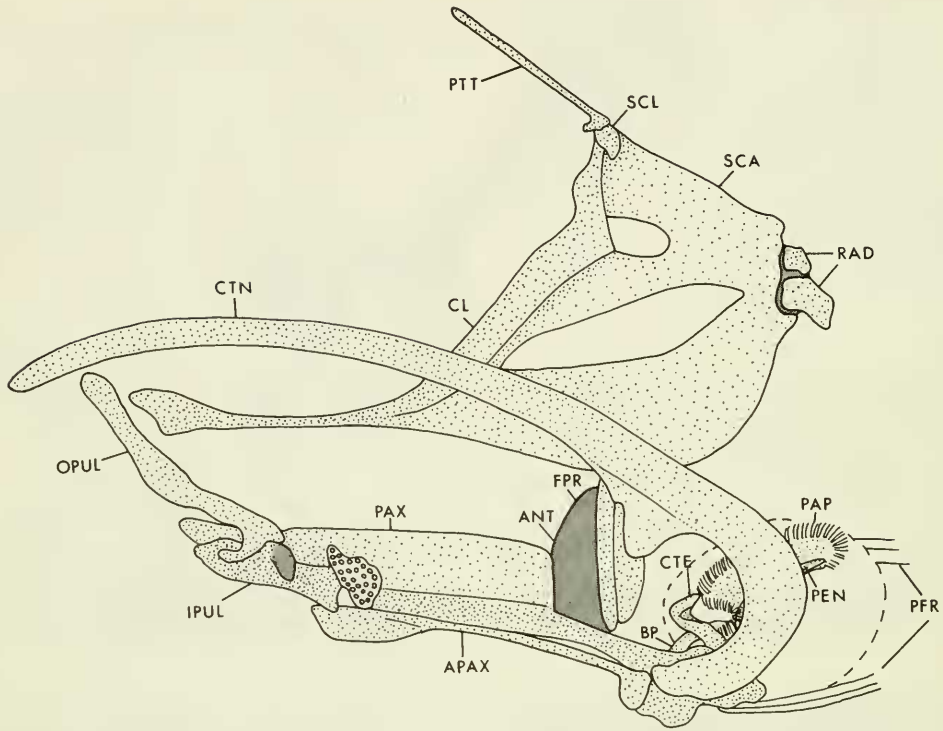


FIGURE 3. Diagrammatic representation of modified pelvic and pectoral fins in priapium of a sinistral male, *Neostethus lankesteri* (CAS-SU 67162). Anterior to left. Dense stippling, cartilage; light stippling, bone. Open circles, fibrous connective tissue of pulvinular appendage. Dotted line approximates outline of epididymis. Abbreviations: apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; cte, second ctenactinium; ctan, first ctenactinium; fpr, first pleural ribs; ipul, inner pulvinular bone; opul, outer pulvinular bone; pap, papillary bone; pax, proctal axial bone; pen, penial bone; pfr, pelvic fin rays; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum.

and inserts on the base of the papillary bone.

inner muscle of the proctal side (Fig. 6)—Regan (1916:14). An elongate muscle that originates at the junction of the main crest of the proctal axial bone, internal to the outer muscle of the aproctal side, and inserts on a process of the proximal end of the toxactinium or outer pulvinular bone. muscle of the proctal side (Fig. 6)—Regan (1916:14). A muscle that originates at the extreme anterior end of the axial bone, with a few fibers at the posterior base of the toxactinium, posteriorly produced into a long tendon that inserts on the base of the papillary bone.

papillary bones (Figs. 2–4)—Regan (1916:8), Parenti (1984:6). Five small posterior priapial bones. Synonym: penial bones (Bailey 1936:467).

penial bone (Figs. 2–4)—Bailey (1936:467).

A thin, laminar bone that projects into the seminal papilla.

basipenial bone (Figs. 2–4)—Bailey (1936:465, 468). A rodlike bone that articulates with the base of the penial bone and posterior border of the cristate bone.

papillary bone (Figs. 2–4)—Regan (1916:8), Bailey (1936:468), Herre (1939:143). A slender, curved bone that supports the seminal papilla.

prepapillary bone (Fig. 2)—Bailey (1936:468). A slender, rodlike bone that articulates proximally with the basipenial bone and distally with the papillary bone.

cristate bone—Bailey (1936:469). A flattened, platelike bone that lies between the papillary bone and the aproctal axial bone and projects into the base of the seminal papilla.

pleuro-priapial muscle (Fig. 6)—Regan (1916:12).

A thin muscle that originates on the enlarged

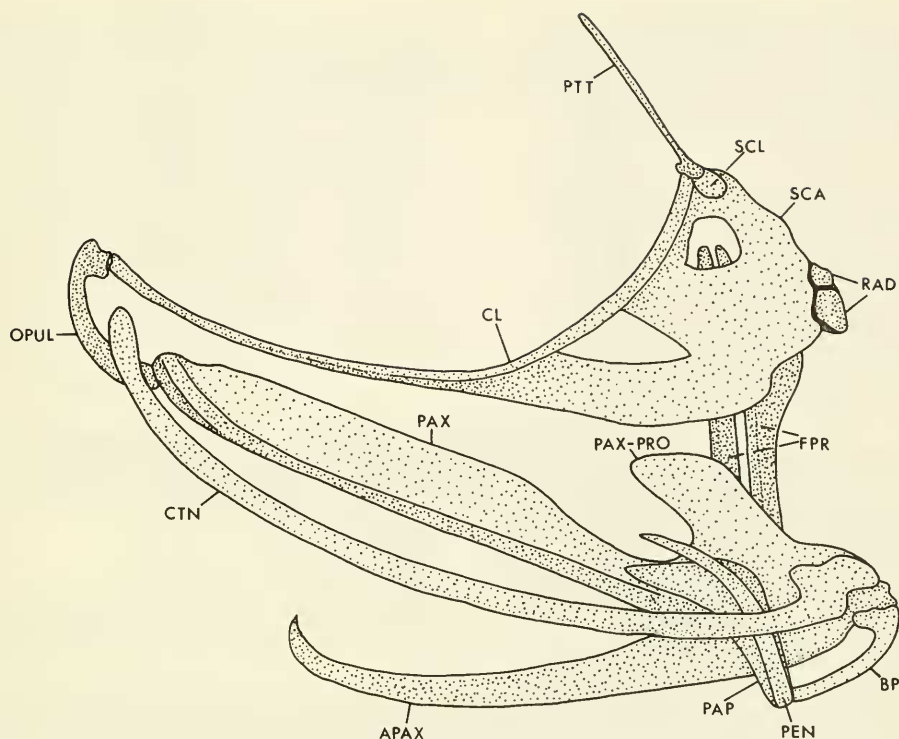


FIGURE 4. Diagrammatic representation of modified pelvic and pectoral fins in priapium of a sinistral male, *Gulaphallus mirabilis* (CAS-SU 38904 and modified in part from Bailey 1936). Anterior to left. Dense stippling, cartilage; light stippling, bone. Abbreviations: apax, aproctal axial bone; bp, basipenial bone; cl, cleithrum; ctan, first ctenactinium; fpr, first pleural ribs; opul, outer pulvinular bone; pap, papillary bone; pax, proctal axial bone; pax-pro, process of the proctal axial bone; pen, penial bone; ptt, posttemporal bone; rad, radials; sca, scapulocoracoid; scl, supracleithrum.

transverse process of the third or fourth vertebra on the proctal side and inserts on the proctal axial bone at the point of articulation of the first ctenactinium.

priapial process of cleithra (Figs. 3, 4)—Regan (1913:553–554). Anterior prolongation of the cleithra in *Neostethus* and *Gulaphallus*.

priapial ribs (Figs. 2–4)—Bailey (1936:463–464). The first pleural ribs on the third or fourth vertebra, modified to support the priapium.

aproctal priapial rib—Bailey (1936:464). The first pleural rib on the aproctal side of the body.

proctal priapial rib—Bailey (1936:463). The first pleural rib on the proctal side of the body.

priapium (Figs. 2–5, 9)—Regan (1913:551, 1916: 4), Myers (1928:1), Bailey (1936:453), Aurich (1937:263), TeWinkel (1939:59), Woltereck (1942a:254, 1942b:338). The subcephalic cop-

ulatory organ of phallostethid fishes comprising a bony portion used to hold the female during mating, a fleshy copulatory organ or seminal papilla through which sperm bundles

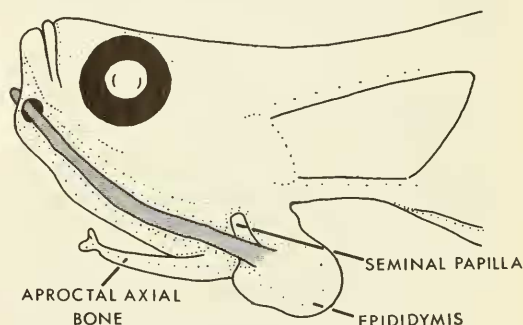


FIGURE 5. Diagrammatic representation of head and anterior portion of body, *Gulaphallus mirabilis*, sinistral male (CAS 50720). Anterior to left. Dense stippling, first ctenactinium.

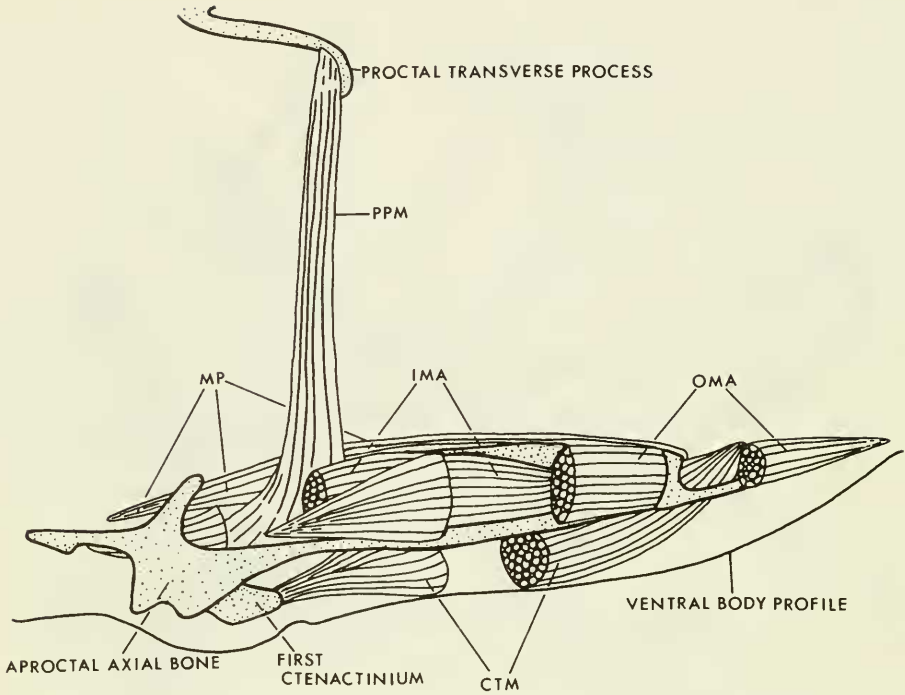


FIGURE 6. Schematic diagram of priapial muscles (modified from Regan 1916:fig. 10). Anterior to right. Stippling, bone. Abbreviations: ppm, pleuro-priapial muscle; ctm, ctenactinial muscle; mp, muscle of proctal side; ima, inner muscle of aproctal side; oma, outer muscle of aproctal side.

pass, and expanded cleithra and pleural ribs for suspension.

proctal side or aspect—Regan (1913:551, 1916:5), Herre (1942:138), Parenti (1986a:233). That side of the body with the anal opening.

pulvinular appendage (Fig. 3)—Regan (1916:5, 8), Herre (1942:137). A subconical, compressed mass of fibrous tissue that lies just posterior to the pulvinulus and is supported by the inner pulvinular bone in *Neostethus*.

pulvinular spine (Fig. 3)—Regan (1916:5, 9). A pointed, curved process of the toxactinium (=outer pulvinular bone).

pulvinular bones (Figs. 2–4)—Regan (1916:8–9). Two bones, termed an inner and an outer pulvinular, that articulate with the anterior end of the proctal axial bone.

inner pulvinular bone (Fig. 3)—Regan (1916:8–9). A longitudinal, chondral bone that lies anteroventral to the proctal axial bone.

outer pulvinular bone (Figs. 2–4)—Regan (1916:9). See toxactinium.

pulvinulus (Figs. 2, 9)—Regan (1916:5, 8), Myers (1928:6, 1935:5), Villadolid and Manacop (1935:194), Manacop (1936:376), Aurich (1937:264), Herre (1939:140), TeWinkel (1939:62), Roberts (1971a:7). Fibrous tissue surrounding the inner pulvinular bone and/or toxactinium (=outer pulvinular bone) covering point of articulation of the toxactinium, cleithra, and proctal axial bone. Synonyms: shieldlike pad (Bailey 1936:454); pulvinular pad (Parenti 1986a:230).

seminal papilla (Fig. 5)—Regan (1916:5), Herre (1939:143). A papilliform projection lying posterior to the infrascular prominence, supported internally by the posterior infrascular bone. Synonyms: genital papilla (TeWinkel 1939:62), penis (Roberts 1971a:1; Parenti 1986a:228).

toxactinium (Figs. 2–4)—Regan (1913:551), Myers (1928:1), Bailey (1936:462), Woltereck (1942b:339), Herre (1939:140, 1942:138), Roberts (1971a:6), Parenti (1986a:228). A rodlike, longitudinal bone, the posterior end

of which movably articulates with the symphysis of the cleithra and anterior end of the proctal axial bone. In *Phallostethus* and *Phenacostethus*, the anterior, distal end curves below the head towards the aproctal side of the body. Called the outer pulvinular bone in all other phallostethids, in which the anterior end articulates with the anterior end of the urohyal and the first basibranchial bone. Synonyms: outer pulvinular bone (Regan 1916:9), pulvinular bone (Bailey 1936:463), toxactinial bone (Bailey 1936:471), inner pulvinular bone (misidentification, Roberts 1971b:393), modified pulvinulus (Parenti 1984:6).

uncus (Fig. 2)—Bailey (1936:465, 467). A U-shaped chondral bone that articulates with the proctal axial bone posteriorly.

PHYLOGENETIC ANALYSIS

External morphology and osteology of the priapium has been reported in detail for a variety of phallostethid species (e.g., Regan 1913, 1916; Bailey 1936; Aurich 1937; TeWinkel 1939; Roberts 1971a, b; and Parenti 1984, 1986a). However, this represents the first attempt to summarize derived priapial and other characters within all phallostethid fishes, and to use corroborated hypotheses of synapomorphies to diagnose monophyletic genera and groups of genera.

Aurich (1937:285) perhaps came the closest to the goal of diagnosing groups of genera by tabulating identifying characters of his three subfamilies (but called "Familien")—Phallostethinae, Neostethinae, and Gulaphallinae—recognized herein at the tribal level with modified definition and composition. Aurich did not treat relationships among his three subfamilies, nor did he indicate which of the listed characters are what we would today recognize as derived or apomorphic.

Herre (1942) provided a synopsis of all genera and species, except *Phallostethus* and *Phenacostethus*, both then monotypic. I find many of Herre's (1942) characters, especially of scales, unworkable in a phylogenetic analysis. For example, number of scales on the opercle was used to divide *Neostethus* species into subgenera *Neostethus* and *Sandakanus*. Herre (1942:153) described several new species, including *N. panayensis*, treated as closely related to *N. zamboangae* Herre, 1942 and *N. coronensis* Herre,

1942, with which it shares two scales on the opercle. However, in priapial morphology, *N. panayensis* is a member of the monophyletic *Gulaphallus* as defined below, and not closely related to *N. zamboangae* or *N. coronensis* (= *borneensis*, herein).

Roberts (1971b:396) published a diagram in which relationships among the then recognized nine genera were summarized. It was not Roberts's purpose to provide a phylogenetic revision of all phallostethids; however, like Herre, Roberts depicted the monotypic *Manacopus* as closely related to *Neostethus*; *Manacopus* is considered a synonym of *Gulaphallus* herein.

Monophyly of Phallostethidae

As stated in the section Relationships of Phallostethids to other Atherinomorphs, phallostethid fishes have been considered monophyletic since Regan's (1916) review of the then three known species: by definition, all phallostethid males have a priapium, a complex structure not found in any other group of fishes. It is perhaps impossible to tabulate all the characters in phallostethids that have undergone transformation from the state in plesiomorphic atherinoids. Over 30 modifications of pelvic and pectoral bones, muscles, and cartilage can be identified (see Synonymy and Homology of Priapial Structures).

Further, presence of a keel, homologous with the ventral embryonic fin-fold as reported by Takita and Nakamura (1986) in larval *Hypoatherina bleekeri*, and other paedomorphic characters in all phallostethids suggest that evolution of a priapium is correlated with maturation at a relatively small size. Congruence (Mickeyevich 1978) exists between patterns of loss and reduction associated with small size and development of some complex priapial characters, especially within phallostethins.

Relationships of Subfamilies and Tribes

The following classification summarizes phylogenetic relationships among the tribes and subfamilies of phallostethids I recognize:

- Family Phallostethidae
 - Subfamily Phallostethinae
 - Tribe Phallostethini
 - Tribe Neostethini
 - Subfamily Gulaphallinae
 - Tribe Gulaphallini

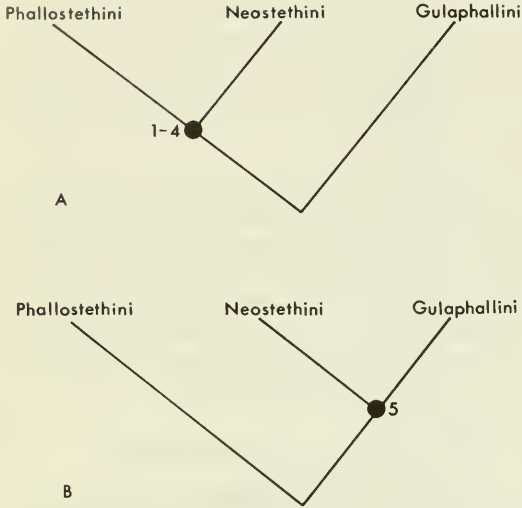


FIGURE 7. Two alternative cladograms of relationships among the three phallostethid tribes. Characters numbered as in Phylogenetic Analysis.

I use the following vernacular terms: phallostethins for Phallostethini, neostethins for Neostethini, and gulaphallins for Gulaphallini. To avoid confusion, no vernacular is used for Phallostethinae. Monophyly of each tribe is considered below. Two alternative relationships are: Phallostethini and Neostethini are sister tribes (Fig. 7a); and Neostethini and Gulaphallini are sister tribes (Fig. 7b). I have found no support for the hypothesis that Gulaphallini and Phallostethini are sister tribes; that possible phylogeny will not be discussed further.

The first alternative is supported by at least four derived characters, two of the priapium, one of the oral jaws, and one of the gill arches. Characters have the same numbers as in the cladograms of Figures 7, 8, and 11.

1. Second ctenactinium present (Figs. 2, 3, 9).

The second ctenactinium is a small, curved, externalized priapial bone that may have bony serrations (Regan 1916:fig. 3). It is present in *Neostethus* (Figs. 3, 9) and *Phallostethus*, and is rudimentary in *Phenacostethus* (Fig. 2). The bone is absent in *Gulaphallus* (Fig. 4), contrary to Aurich (1937) who misidentified the large, partially externalized papillary bone as a second ctenactinium.

2. Shieldlike pulvinulus present (Figs. 2, 9) and outer pulvinular bone robust (Figs. 2, 3).

The oval pulvinulus of *Phallostethus*, *Phena-*

costethus (Fig. 2), and *Neostethus* (Fig. 9) forms a shieldlike covering of the articulation point between the outer pulvinular and proctal axial bones. The outer pulvinular bone, although present in gulaphallins (Fig. 4), is larger and more robust in phallostethins and neostethins. Bailey (1936) and Aurich (1937) reported a slender, long pulvinulus paralleling the longitudinal ctenactinial muscles in *Gulaphallus*. However, the structure in *Gulaphallus* appears to be simply a fold of skin covering the muscles and is viewed here as doubtfully homologous with the distinctive pulvinulus of neostethins and phallostethins.

3. Highly protrusible oral jaws.

Premaxillary ascending processes are long, and a short, rodlike block (submaxillary element of Parenti 1984) lies between the maxilla and vomer in Neostethini and Phallostethini, both characters contributing to the highly protrusible oral jaws (Roberts 1971b; Ivantsoff et al. 1987). The block may be ossified in *Phallostethus* and some species of *Neostethus*; otherwise it is cartilaginous. In Gulaphallini, there is a thin connective tissue meniscus between the maxilla and vomer, except in *G. panayensis* in which the meniscus is enlarged.

4. Reduction of hyobranchial apparatus.

The entire hyobranchial apparatus is reduced in phallostethids relative to other atherinoids (see Rosen and Parenti 1981). Teeth on the fourth ceratobranchial toothplate are few or absent in phallostethins and neostethins; they are present in outgroup taxa such as *Dentatherina merceri* and *Pseudomugil signifer*, as well as in *Gulaphallus*.

The alternative that Neostethini and Gulaphallini are sister tribes is supported by what may be described as one complex priapial character.

5. Anterior elongation of priapial suspensory system, including anteriorly expanded cleithra and transverse processes of fourth vertebrae of males, with the proctal transverse process larger than the slightly modified aproctal transverse process (Figs. 3, 4), and elongate first ctenactinium, the prominent externalized priapial bone (Figs. 3, 4, 9).

Parsimony may be used to choose the first phylogenetic hypothesis (Fig. 7a) over the second (Fig. 7b), but that criterion alone is not satisfactory. Outgroup comparison is of limited use in deciding polarity of priapial structures, and likewise, complex priapial characters may be treated

as one or several characters. I choose the hypothesis that Phallostethini and Neostethini are sister tribes for reasons of parsimony and also because derived characters other than those of the priapium are shared. This hypothesis requires that anterior elongation of the priapium in neostethins and gulaphallins (character 5, above) be viewed as plesiomorphic for all phallostethids.

Monophyly of Tribes

Phallostethini.—Four characters distinguish phallostethins from all other phallostethids.

6. A large, fleshy seminal papilla.

The seminal papilla is enlarged relative to the papilla in neostethins or gulaphallins (Fig. 5). The large papilla may be smooth (Roberts 1971a: fig. 5) or ruffled (Roberts 1971a: fig. 4). An enlarged seminal papilla refutes the hypothesis that the diminutive phallostethins can be described solely as paedomorphic phallostethids.

7. The curved toxactinium the largest externalized bony priapial element (Fig. 2).

Treating the distinctive curved toxactinium as a derived character of *Phallostethus* and *Phenacostethus* is consistent with the interpretation (above) that the elongate ctenactinium and anterior elongation of the priapium in neostethins and gulaphallins are primitive for phallostethids.

8. Extremely small and delicate, with deciduous scales.

The largest phallostethid, *Gulaphallus eximius*, reaches a recorded 37 mm SL (see character 47, below). TeWinkel (1939) gives an unsupported range of 14–40 mm SL. Neostethins and gulaphallins generally mature at over 20 mm SL; the exception, *N. borneensis*, is considered secondarily reduced. Small adult size and the deciduous scales of phallostethins are probably paedomorphic characters correlated with character 9.

9. A translucent, membranous dome on dorsal surface of head.

The membranous dome (Roberts 1971a: figs. 2, 3) on the dorsal surface of the head may best be described as a larval characteristic of atherinoids (as in *Hypoatherina bleekeri*; see Takita and Nakamura 1986) retained in adults.

Neostethini.—Two characters distinguish *Neostethus* from all other phallostethids.

10. An inner pulvinular bone (Fig. 3).

The inner pulvinular bone is a large, well-developed chondral bone lying just posterior to, and articulating with, the outer pulvinular bone. It has no identified homolog in phallostethins or gulaphallins.

11. A high number of thin, bony projections on the papillary bone (Fig. 3).

The papillary bone has a high number (reportedly more than 80; Roberts 1971b) of thin, bony projections in *Neostethus* (Aurich 1937: fig. 6). These are the projections used by Myers (1935) to diagnose a new genus, *Plectrostethus* (= *Neostethus*, herein). Myers apparently compared his new species with phallostethins and gulaphallins, which lack projections. In the neostethins, *Neostethus thessa* and *N. zamboangae*, the papillary bone has only rudimentary projections.

Gulaphallini.—*Gulaphallus* species are together distinguished from all other phallostethids by three derived characters.

12. A perforated gular flap of skin through which the anterior end of the first ctenactinium may pass and remain while at rest (Fig. 5; Aurich 1937: fig. 2).

Neostethins are the other group of phallostethids with an elongate first ctenactinium; however, neostethins do not possess a large gular flap through which the anterior end of the ctenactinium may pass. This character, mentioned and figured by Aurich (1937: fig. 2), is uniquely derived in *Gulaphallus*.

13. The apical axial bone projects beyond ventral body profile (Figs. 4, 5).

In no other phallostethids does a priapial bone project beyond the body profile and away from the body of the priapium.

14. A small, dorsal crest posteriorly on proctal axial bone (Fig. 4).

In other phallostethids (Figs. 2, 3) the proctal axial bone has a uniform dorsal outline.

Species Relationships Within Tribes

Phallostethini

Relationships among, and definitions of, the four phallostethin species *Phallostethus dunckeri*, and *Phenacostethus smithi*, *P. posthon*, and *P. trewavasae* were treated in detail by Parenti (1986a) and need not be repeated here. Defining characters of each species are listed in the Systematic Accounts.

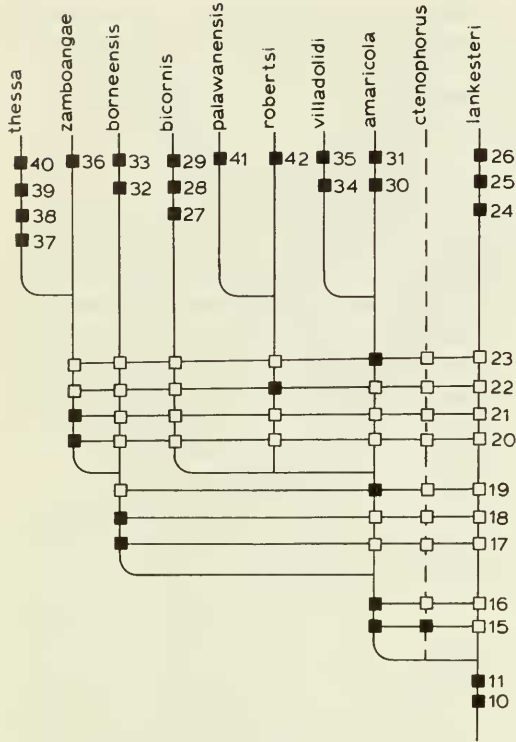


FIGURE 8. Cladogram of relationships among species in the Neostethini. Solid squares, synapomorphies; open squares, symplesiomorphies. Characters numbered as in Phylogenetic Analysis.

Neostethini

Hypothesized relationships among the ten *Neostethus* species are depicted in Figure 8. *Neostethus lankesteri* is considered to be the most plesiomorphic neostethin; it is excluded from a monophyletic group comprising *Neostethus amaricola*, *N. villadolidi*, *N. robertsi*, *N. palawanensis*, *N. bicornis*, *N. borneensis*, *N. zamboangae*, and *N. thessa*, defined by two shared derived characters.

15. An enlarged, prominent, second ctenactinium.

Presence of a second ctenactinium is treated as a derived character of neostethins and phallostethins (see character 1, above). The second ctenactinium is a small curved bone in phallostethins (Fig. 2) and *N. lankesteri* (Fig. 3). It is a much larger, prominent, externalized priapial bone in all other species of *Neostethus*, including *N. ctenophorus*, as illustrated by Aurich (1937: fig. 6). Variation in shape of the second ctenac-

tinium and in its association within other priapial structures is the primary source of information on morphological species recognition within neostethins.

16. A short, bladelike aproctal axial bone.

The aproctal axial bone is nearly as long as the proctal axial bone and reaches the pulvinulus in phallostethins (Fig. 2), *Neostethus lankesteri* (Fig. 3), *N. ctenophorus* (Aurich 1937:fig. 6), and *Gulphallus* (Fig. 4). In all other species of *Neostethus* (Roberts 1971b:fig. 12), the aproctal axial bone is shortened and somewhat bladelike; it does not reach the pulvinulus.

Neostethus ctenophorus, of which no specimens are available, is treated as forming an unresolved trichotomy with *N. lankesteri* and all other *Neostethus* (Fig. 8). I divide these remaining species of *Neostethus* into two monophyletic groups, which I call the *borneensis* and the *bicornis* groups, diagnosed as follows:

The *borneensis* group, comprising *Neostethus borneensis*, *N. thessa*, and *N. zamboangae*, is diagnosed by two shared derived characters that could be treated as one complex priapial character.

17. Strongly curved, thin, second ctenactinium.

The second ctenactinium is a strongly curved, thin bone (Aurich 1937:fig. 4) as opposed to being a stout fin ray as in *Neostethus amaricola* and *N. villadolidi* (Fig. 9) and *N. bicornis* (Roberts 1971b: fig. 12).

18. Papillary and penial bones curved and elongate, lying parallel to dorsal surface of second ctenactinium.

Position of the papillary and penial bones just dorsal to the second ctenactinium means that the seminal papilla (supported by the papillary and penial bones) empties just dorsal to the second ctenactinium, as opposed to a more posterior position in those phallostethids with smaller papillary and penial bones.

The *bicornis* group, comprising *Neostethus bicornis*, *N. palawanensis*, *N. robertsi*, *N. amaricola*, and *N. villadolidi*, is diagnosed by one complex, derived character.

19. Both the proctal and aproctal transverse processes of the fourth vertebra in males are enlarged and oriented anteriorly.

It was concluded (character 5, above) that the anterior elongation of the entire priapial apparatus is a plesiomorphic character for phallostethid fishes. This character complex is modi-

fied in the *bicornis* group such that the aproctal as well as the proctal transverse processes of the fourth vertebra in males are drawn so far anteriorly that the anterior tip of both processes lies parallel to the first vertebra.

Within the *borneensis* group, *Neostethus borneensis* is considered plesiomorphic to *N. thessa* and *N. zamboangae*, diagnosed as sister species by sharing two derived characters.

20. Anterior aproctal ossification present.

In all species of *Neostethus* except *N. lankesteri*, the aproctal axial bone is short and does not reach the pulvinulus (see character 16, above). In *N. thessa* and *N. zamboangae*, there is a thin, elongate ossification just anterior to the aproctal axial bone but separate from it. Aurich (1937: fig. 4) figured the aproctal axial bone and anterior aproctal ossification as one long bone. A similar bone in *N. bicornis* was called the "pulvinular osselet" by Roberts (1971b:fig. 12). However, because of differences in size and shape of the bones, I do not consider that minute ossification in *N. bicornis* to be homologous with the ossification in *N. thessa* and *N. zamboangae*.

21. Reduction in number of papillary projections.

The thin, elongate papillary and penial bones of the *borneensis* group (character 18, above) are even further reduced within *N. thessa* and *N. zamboangae* so that the fine, bony projections of the papillary bone (Fig. 3) are few or absent.

Within the *bicornis* group, I recognize a trichotomy among *N. bicornis* and two sister-group pairs, *N. palawanensis* and *N. robertsi*, and *N. villadolidi* and *N. amaricola*.

Neostethus palawanensis and *N. robertsi* share one derived character.

22. Claw-shaped, anteriorly bifurcated, second ctenactinium (Fig. 13).

The anterior extent of the second ctenactinium in all other phallostethids that have the bone is either blunt (Fig. 3) or sharply pointed (Fig. 9). Hence, the claw-shaped, anteriorly bifurcated second ctenactinium of *N. palawanensis* and *N. robertsi* (Fig. 13), much larger and better developed in the latter species, is judged to be uniquely derived within phallostethids.

Neostethus villadolidi and *N. amaricola* share one derived character.

23. Sharply pointed second ctenactinium (Fig. 9).

Neostethus villadolidi and *N. amaricola* are two small, narrow-bodied phallostethid species dis-

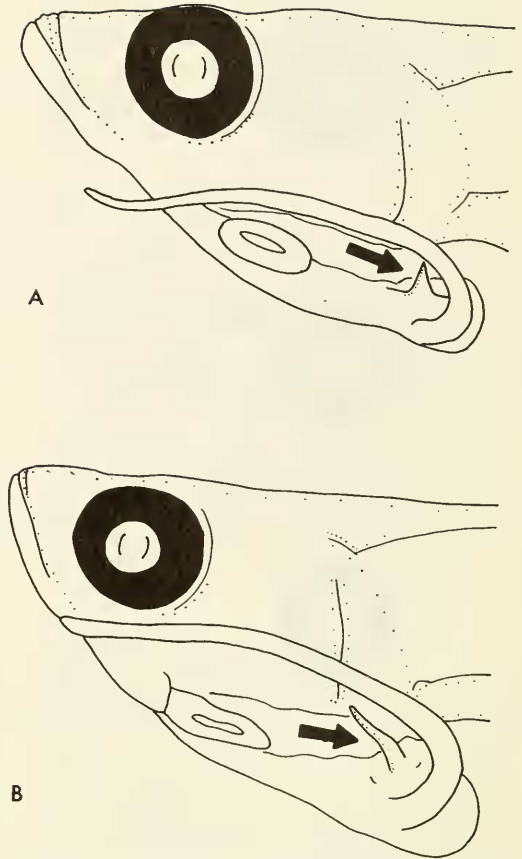


FIGURE 9. Diagrammatic representation of head and anterior portion of body, a. *Neostethus villadolidi*, sinistral male, CAS 60258, b. *Neostethus amaricola*, sinistral male, CAS-SU 38898. Anterior to left. Arrow points to second ctenactinium.

tinguished from all other phallostethids by their sharply pointed, either anteriorly or dorsally directed, second ctenactinia.

Autapomorphies of Each Species of *Neostethus*

Neostethus lankesteri

24. Males with a small, slightly pointed, triangular, ventral bony projection on the elongate first ctenactinium (Fig. 3).

The first ctenactinium is an elongate, uniformly rod-shaped bone in all other phallostethids in which it occurs. *Neostethus lankesteri* is unique among phallostethids in having a small, slightly pointed, triangular, bony projection on the ventral surface of the first ctenactinium (Fig. 3).

25. Distal tips of the first pleural ribs project beyond ventral outline of priapium.

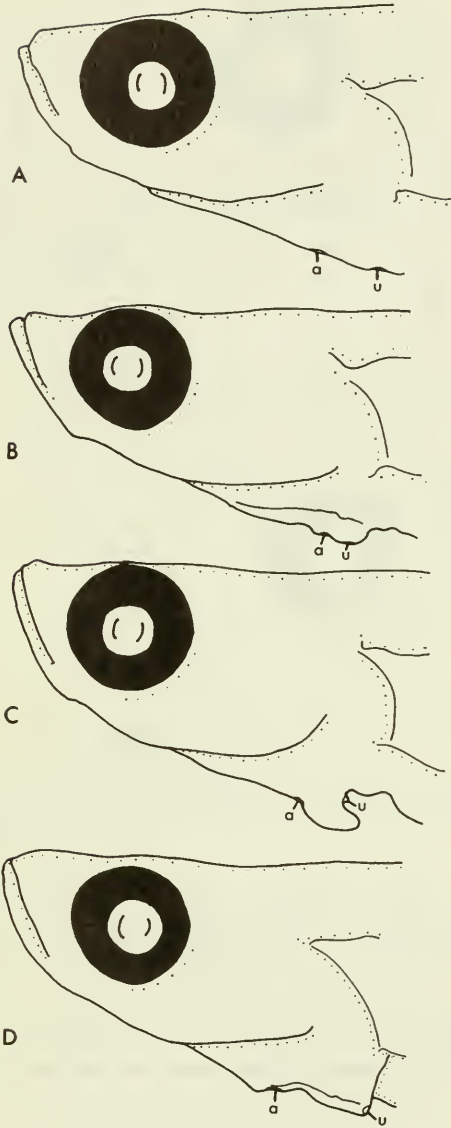


FIGURE 10. Diagrammatic representation of head and anterior portion of body, adult female, a. *Neostethus thessa* (CAS-SU 36546), b. *Neostethus villadolidi* (CAS 60258), c. *Neostethus lankesteri* (CAS-SU 67162), d. *Neostethus bicornis* (CAS 35783). Abbreviations: a, anus; u, urogenital opening.

The first pleural ribs in all phallostethid males are offset to the proctal side of the priapium (Fig. 3). In *N. lankesteri*, the distal tips of the ribs project beyond the ventral outline of the priapium when it is viewed from the proctal side.

26. Females have a large, hooklike, urogenital papilla (Fig. 10c).

In all female phallostethids, the anus is ante-

rior to the urogenital openings (Fig. 10). Most species are like *N. thessa* (Fig. 10a), in which females have no anal or urogenital papilla or covering. Adult female *N. lankesteri* are readily distinguished from all other phallostethid females by a large, hooklike papilla that lies posterior to the anal opening and anterior to the urogenital openings, towards which it curves (Fig. 10c).

Neostethus bicornis

27. Mature males with two, elongate ctenactinia.

The second ctenactinium of *N. bicornis* is the longest of any phallostethid, at least one-half the length of the first ctenactinium in adult males (Roberts 1971b:fig. 12).

28. Immature males with a brown blotch on the proctal pelvic rays that fades with growth and maturity.

Immature males can be readily identified as sinistral or dextral (see Parenti 1986a and character 44, below) by a small brown blotch present on the proctal pelvic fin rays. This blotch becomes diffuse, hence less recognizable, with growth.

29. Females with a fleshy, hoodlike flap covering the urogenital openings (Fig. 10d).

Adult female *N. bicornis* are readily distinguished from all other phallostethids by the presence of a unique fleshy, hoodlike flap that extends from the anus to the urogenital openings (Fig. 10d). Although females of *N. lankesteri* and *N. bicornis* have fleshy coverings of the urogenital openings, I do not recognize this as a shared derived character because form of the urogenital covering is different in the two species, and numerous other characters refute a close relationship between the two.

Neostethus amaricola

30. Distal tips of the first pleural ribs of females project beyond the ventral body profile.

Herre (1942:148) used "Female with two spurs or papillae on sides of throat" as a key character of *N. amaricola*. The spurs or papillae are the distal tips of the first pleural ribs that project beyond the ventral body profile on either side of the urogenital openings.

31. A sharply pointed, anteriorly directed, second ctenactinium (Fig. 9b).

Males of *N. amaricola* are readily distin-

guished from those of its sister species, *N. villadolidi*, by a sharply pointed second ctenactinium that is directed anteriorly (Fig. 9).

Neostethus borneensis

Neostethus borneensis is a relatively short-bodied species that is distinguished from all other neostethins by two, probably correlated, characters (see *G. panayensis*, below, for a similar definition).

32. Low number of vertebrae (31–32) (Table 2) in males and females.

Vertebrae in other species of *Neostethus* range from 34 to 37 (Table 2), in *Gulaphallus* from 35 to 37, except for *G. panayensis* in which the number of vertebrae is also reduced, and in phallostethins from 33 to 40 (Table 2). Vertebrae number 40–43 in *Dentatherina merceri* (fide Patten and Ivantsoff 1983:332), and 29–30 in *Pseudomugil signifer* (CAS 62565), two outgroup species. The plesiomorphic vertebral number for phallostethids is ambiguous. I treat the vertebral number in *N. borneensis* as derived because it is low compared to all other neostethins and phallostethins.

33. Low number of scales in a lateral series (25–27) (Table 2) in males and females.

Scales in a lateral series in other species of *Neostethus* range from 29 to 34, and in *Gulaphallus* from 28 to 58 (Table 2). Scales in a lateral series number 40–43 in *Dentatherina merceri* (fide Patten and Ivantsoff 1983:332), and 29–32 in *Pseudomugil signifer* (CAS 62565), two outgroup species. The plesiomorphic number of scales in a lateral series in phallostethids is ambiguous. I hypothesize that the number in *N. borneensis* is derived because it is low compared to outgroup species and other phallostethids.

Neostethus villadolidi

34. A fleshy urogenital protuberance (Fig. 10b) in females.

Adult female *N. villadolidi* have a fleshy protuberance just posterior to the anus and anterior to the urogenital openings. It could be described as an incipient or rudimentary papilla; however, I do not recognize a transition series from the state of the urogenital papilla in *N. lankesteri* or the urogenital flap in *N. bicornis*, as discussed above for character 29.

35. A sharply pointed, dorsally directed second ctenactinium (Fig. 9a).

Male specimens of *N. villadolidi* are readily distinguished from male specimens of *N. amari-cola*, its proposed sister species, by a sharply pointed second ctenactinium that is directed dorsally (Fig. 9).

Neostethus zamboangae

36. A small, hooked, second ctenactinium with two to seven bony serrations.

Neostethus zamboangae adult males have two to seven bony serrations on the ventral surface of the hooked second ctenactinium. Regan (1913: figs. 1, 3) illustrated serrations on what I identify as the second ctenactinium in *Phallostethus dunckeri*; however, I do not propose a close relationship between *N. zamboangae* and *P. dunckeri* because other characters lead me to conclude that they are members of different, monophyletic tribes.

Neostethus thessa

37. Absence of first dorsal fin rays and most of the first dorsal pterygiophore in males and females.

The first dorsal fin is absent in three phallostethid species: *N. thessa*, *Phallostethus dunckeri* (Parenti 1986a), and *Gulaphallus bikolanus*. I view this absence as the individual loss of the first dorsal fin in each species. A first dorsal fin is plesiomorphic for atherinomorphs, being present in outgroups *Bedotia*, *Melanotaenia*, *Hypopotherina*, *Dentatherina*, and *Pseudomugil* and all other phallostethids. Each of the three phallostethid species that lacks a first dorsal fin is a member of its own well-corroborated monophyletic group, and a remnant of the first dorsal pterygiophore is present in some specimens.

38. Oral dentition reduced to several small unicuspid teeth on premaxilla and dentary in males and females.

Oral teeth, in one or two rows in other *Neostethus* species, are reduced to a few randomly distributed unicuspid teeth in *N. thessa*.

39. A relatively long anal fin (17–22 rays) (Table 2) in males and females.

Anal fin rays in other *Neostethus* and *Gulaphallus* number from 13 to 18 (Table 2), in *Phenacostethus* from 14 to 15 (Table 2). *Phallostethus dunckeri* is the one other phallostethid species having a relatively long anal fin with 26–28 rays (Table 2). In one outgroup species, *Dentatherina*

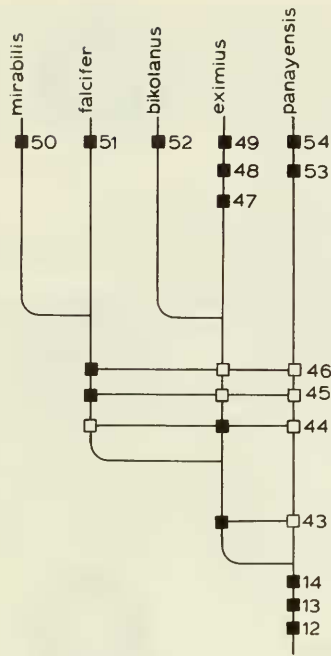


FIGURE 11. Cladogram of relationships among species in the Gulaphallini. Solid squares, synapomorphies; open squares, symplesiomorphies. Characters numbered as in Phylogenetic Analysis.

merceri, anal fin rays number from 15 to 17 (Patten and Ivantsoff 1983).

40. A relatively long second dorsal fin (8–10 rays) (Table 2) in males and females.

Second dorsal fin rays in other *Neostethus* range from 5 to 7, in *Gulaphallus* from 6 to 8, in *Phenacostethus* from 5 to 7, and in *Phallostethus*, 8–10 (Table 2). Absence of the first dorsal fin and increase in the number of second dorsal fin rays in both *N. thessa* and *P. dunckeri* invites speculation that the two dorsal fins have become confluent in development. However, absence of the first dorsal fin in *Gulaphallus bikolanus* with no increase in number of second dorsal fin rays refutes this as a general phenomenon in phallostethids.

Neostethus palawanensis

41. A relatively straight first ctenactinium with a broad, fleshy ventral ridge.

The first ctenactinium is the prominent externalized priapial bone in neostethins and gulaphallins (see character 5, above). It is typically a

long, slender, curved bone (Figs. 3, 4) except in *N. palawanensis* in which it is relatively straight and has a thick, fleshy ventral ridge (Myers 1935). I consider the fleshy ventral ridge uniquely derived in *N. palawanensis*.

Neostethus robertsi

42. A large, well-developed, claw-shaped second ctenactinium (Fig. 12).

Neostethus robertsi and *N. palawanensis* are considered sister species because they share the uniquely derived character of a claw-shaped, anteriorly bifurcated, second ctenactinium (see character 22, above). The claw-shaped second ctenactinium is much larger and better developed in *N. robertsi* than in *N. palawanensis*.

Neostethus ctenophorus

There are no identifiable autapomorphies of *N. ctenophorus* (see Systematic Accounts).

Gulaphallini

Relationships among the five *Gulaphallus* species are depicted in Figure 11. Four species, *G. eximius*, *G. mirabilis*, *G. falcifer*, and *G. bikolanus*, are considered to be most closely related because they share one derived character.

43. Large, well-developed aproctal axial bone (Fig. 4).

The aproctal axial bone is relatively large and has a well-developed dorsal and ventral ridge in *G. eximius*, *G. mirabilis*, *G. falcifer*, and *G. bikolanus* (Fig. 4), as opposed to the condition in *G. panayensis* in which the bone is thin and elongate.

Gulaphallus bikolanus and *G. eximius* are considered sister species because they share one derived character.

44. Adult males exclusively dextral.

All adult male phallostethids are bilaterally asymmetric: a sinistral male has the seminal papilla offset to the left side of the body and the anus offset to the right (Parenti 1986a). The reverse is true for dextral males. Sinistral and dextral males occur in about equal numbers in all phallostethid species except the sister species *Phenacostethus trewavasae*, which is sinistral, *Phenacostethus posthon*, which is dextral, and the two species of *Gulaphallus*. I (Parenti 1986a) reviewed the phenomenon of bilateral asymmetry

in phallostethids and speculated that the *Phenacostethus* sister species evolved from an ancestral species in which there were both sinistral and dextral males and concluded that such statements of ancestry are untestable. My hypothesis that *G. eximius* and *G. bikolanus* are sister species because males of each are exclusively dextral does not refute this argument about speciation. The proposal requires that the common ancestor of the two *Gulaphallus* species was exclusively dextral. If that ancestral species had an exclusively sinistral sister species, it is unknown to us now.

Gulaphallus mirabilis and *G. falcifer* are considered to be sister species because they share two derived characters.

45. Antepleurale element ossified in males and females.

The antepleurale cartilage surrounds the distal tips of the first pleural ribs. It is ossified in *G. mirabilis* and *G. falcifer* and cartilaginous in other species of *Gulaphallus*.

46. A brown blotch (concentration of melanophores) at midventral surface just anterior to anal fin in males and females.

Parenti (1986b) used this pigmentation pattern as an identifying character of *G. falcifer*. However, it is found also in *G. mirabilis* and hence used as a derived character to support a close relationship between the two species.

Autapomorphies of Each Species of *Gulaphallus*

Gulaphallus eximius

47. Relatively large body size and scales in a lateral series more than 50 (range 52–58) (Table 2) in males and females.

Gulaphallus eximius is the largest known phallostethid, reaching a recorded 37 mm SL (Herre 1942). Although large size may be considered plesiomorphic for phallostethids, *G. eximius* is perhaps best described as secondarily large. One possible sister taxon, *Dentatherina merceri*, is relatively small, maturing at under 25 mm SL (Patten and Ivantsoff 1983). Correspondingly, *G. eximius* has a high number of scales in a lateral series, ranging from 52 to 58, as opposed to a range of 25–34 for all other neostethins and gulaphallins except *G. mirabilis* (see character 50, below). Also, outgroup species, *D. merceri* and *Pseudomugil signifer* have fewer scales than does *G. eximius* (see character 33, above).

48. A brown blotch (concentration of melanophores) surrounds the anus and urogenital openings in immature females.

This pigmentation pattern is not found in other phallostethids nor in outgroup species and, therefore, is considered uniquely derived in *G. eximius*.

49. Rudimentary pelvic girdle represented by two small scale-like discs of bone in adult females.

Just posterior to the urogenital openings in females is a pair of ossified discs inferred to be a rudimentary pelvic girdle. Similar pelvic girdle elements are found in adult female *Phenacostethus posthon* (see Parenti 1986b:fig. 4).

Gulaphallus mirabilis

50. Scales in lateral series range from 36 to 38 (Table 2).

The high number of scales in a lateral series in *G. mirabilis* is judged to be an independent increase (see character 47, above).

Gulaphallus falcifer

51. Adult females with an elongate pelvic fin ray projecting beyond body profile on either the left or right side of the urogenital opening.

Parenti (1986b) described development of the elongate asymmetric bony element in females of *G. falcifer*, concluding that it is homologous with a pelvic fin ray, not a postcleithrum. *Gulaphallus falcifer* is the only phallostethid in which bilateral asymmetry has been described in females.

Gulaphallus bikolanus

52. First dorsal fin absent in males and females.

Absence of the first dorsal fin in *G. bikolanus* is hypothesized to be independent of its absence in *N. thessa* and *P. dunckeri* (see character 37, above) for reasons of parsimony.

Gulaphallus panayensis

Gulaphallus panayensis is a relatively small *Gulaphallus* species defined by two, probably correlated, characters (see *N. borneensis*, above, for a similar definition).

53. A low number of vertebrae (31–33) (Table 2) in males and females.

The low number of vertebrae in *G. panayensis* is considered a reduction from a higher, plesio-morphic number for phallostethids (see character 32, above).

54. A low number of scales in a lateral series (28–30) (Table 2) in males and females.

The low number of scales in a lateral series is considered a reduction from a higher, plesio-morphic number for phallostethids (see character 33, above).

KEY TO PHALLOSTETHIDAE

The following key is based primarily on characters discussed in the Phylogenetic Analysis. However, characters used to identify the species of *Phallostethus* and *Phenacostethus* are from Parenti (1986a).

- 1A. Second ctenactinium present (Figs. 2, 3, 9); shieldlike pulvinulus present (Figs. 2, 9); outer pulvinular bone robust (Figs. 2, 3); oral jaws highly protrusible; few or no teeth on fourth ceratobranchial toothplate; no perforation in skin of gular region; aproctal axial bone does not project beyond ventral body profile; no dorsal crest on proctal axial bone *Phallostethinae* 2A
- 1B. No second ctenactinium; no pulvinulus; outer pulvinular bone small; oral jaws not highly protrusible; teeth on fourth ceratobranchial toothplate; perforated gular flap of skin through which anterior end of first ctenactinium may pass (Fig. 5); aproctal axial bone projects beyond ventral body profile (Figs. 4, 5); small, dorsal crest posteriorly on proctal axial bone (Fig. 4) *Gulaphallini* 15A
- 2A. Large, fleshy, smooth or ruffled, seminal papilla; large, externalized, curved toxactinium; translucent, membranous dome on dorsal surface of head; no inner pulvinular bone; no bony projections on papillary bone *Phallostethini* 3A
- 2B. Seminal papilla small; no externalized toxactinium; no translucent, membranous dome on dorsal surface of head; inner pulvinular bone present (Fig. 3); high number of thin, bony projections on papillary bone (Fig. 3) or just rudimentary projections *Neostethini* 6A
- 3A. Anal fin rays 26–28; vertebrae 40; second ctenactinium serrated; oral jaws equal; no first dorsal fin; second dorsal fin rays 8–10 *Phallostethus dunckeri* (p. 267)
- 3B. Anal fin rays 14–15; vertebrae 33–35; second ctenactinium greatly reduced and not serrated; lower oral jaw projects beyond upper oral jaw; first dorsal fin ray 1; second dorsal fin rays 5–7 *Phenacostethus* 4A
- 4A. Distal end of seminal papilla ruffled; slightly curved toxactinium (Fig. 2), penial bone present *Phenacostethus smithi* (p. 268)
- 4B. Distal end of seminal papilla smooth; greatly curved toxactinium; penial bone absent 5A
- 5A. First dorsal fin origin posterior to base of last anal fin ray; males dextral; eye-lens large *Phenacostethus posthon* (p. 268)
- 5B. First dorsal fin origin opposite midpoint of anal fin; males sinistral; eye-lens small to minute *Phenacostethus trewavasae* (p. 268)
- 6A. Second ctenactinium small; small, slightly pointed, ventral bony projection on elongate first ctenactinium (Fig. 3); posterior tips of first pleural ribs project beyond body of priapium; females with large, hooklike genital papilla (Fig. 10c) *Neostethus lankesteri* (p. 269)
- 6B. Second ctenactinium large; ventral margin of first ctenactinium smooth, no pointed projection; posterior tips of first pleural ribs do not project beyond body of priapium; females with urogenital papilla that may be fleshy but does not form distinct hook 7A
- 7A. Long aproctal axial bone, reaches pulvinulus *Neostethus ctenophorus* (p. 272)
- 7B. Short, bladelike aproctal axial bone, does not reach pulvinulus 8A
- 8A. Strongly curved, thin, second ctenactinium; papillary and penial bones curved and elongate, lying parallel to dorsal surface of second ctenactinium; proctal transverse processes of fourth vertebra of males enlarged and oriented anteriorly *borneensis* group 9A
- 8B. Straight, stout, second ctenactinium; papillary and penial bones short and straight; proctal and aproctal transverse processes of fourth vertebra of males en-

- larged and oriented anteriorly *bicornis* group 11A
- 9A. Anterior aproctal ossification present; few or no bony projections on papillary bone; vertebrae 35–37; scales in lateral series 29–34 10A
- 9B. No anterior aproctal ossification; numerous bony projections on papillary bone; vertebrae 31–32; scales in lateral series 25–27 *Neostethus borneensis* (p. 270)
- 10A. Small, hooked, second ctenactinium with 2–7 bony serrations; first dorsal fin rays 2; second dorsal fin rays 5–6; complete row of teeth on premaxilla and on dentary; anal fin rays 15–17 *Neostethus zamboangae* (p. 271)
- 10B. Small, hooked second ctenactinium with no bony serrations; no first dorsal fin; second dorsal fin rays 8–10; several small unicuspid teeth on premaxilla and on dentary; anal fin rays 17–22 *Neostethus thessa* (p. 272)
- 11A. Mature males with two elongate ctenactinia; immature males with brown blotch on proctal pelvic rays; females with fleshy, hoodlike flap covering urogenital openings (Fig. 10d) *Neostethus bicornis* (p. 269)
- 11B. Mature males with one elongate ctenactinium; immature males with clear pelvic rays; urogenital openings of females exposed, not covered by fleshy, hoodlike flap 12A
- 12A. Claw-shaped, anteriorly bifurcated, second ctenactinium 13A
- 12B. Sharply pointed second ctenactinium (Fig. 9) 14A
- 13A. Straight first ctenactinium with broad, fleshy, ventral ridge; small, claw-shaped second ctenactinium *Neostethus palawanensis* (p. 271)
- 13B. Slightly bowed first ctenactinium with smooth ventral outline, no fleshy ridge; large, claw-shaped second ctenactinium (Fig. 13) *Neostethus robertsi* (p. 272)
- 14A. Distal tips of first pleural ribs of females project beyond ventral body profile; sharply pointed, anteriorly directed second ctenactinium (Fig. 9b); no fleshy protuberance anterior to urogenital openings of females *Neostethus amaricola* (p. 270)
- 14B. Distal tips of first pleural ribs of females do not project beyond ventral body profile; sharply pointed, dorsally directed second ctenactinium (Fig. 9a); fleshy protuberance anterior to urogenital openings in females (Fig. 10b) *Neostethus villadolidi* (p. 271)
- 15A. Thin, elongate aproctal axial bone; vertebrae 31–33; scales in lateral series 28–30 *Gulaphallus panayensis* (p. 275)
- 15B. Large, well-developed aproctal axial bone (Fig. 4); 35–37 vertebrae; scales in lateral series 32 or more 16A
- 16A. Males dextral; antepleuralelement cartilaginous in adults; midventral surface with tiny, scattered melanophores .. 17A
- 16B. Males sinistral or dextral; antepleuralelement ossified in adults; brown blotch at midventral surface just anterior to anal fin 18A
- 17A. Scales in lateral series 52–58; brown blotch surrounds anus and urogenital openings in immature females; rudimentary pelvic girdle represented by two small scalelike discs of bone in adult females; first dorsal fin present with rays 1–2 *Gulaphallus eximius* (p. 274)
- 17B. Scales in lateral series 32; anus and urogenital openings in females surrounded by tiny, scattered melanophores; no rudimentary pelvic girdle in adult females; no first dorsal fin *Gulaphallus bikolanus* (p. 275)
- 18A. Scales in lateral series 36–38; pelvic rays do not project beyond ventral body profile *Gulaphallus mirabilis* (p. 274)
- 18B. Scales in lateral series 32; an elongate pelvic fin ray projecting beyond body profile on either the left or right side of urogenital opening in adult females ... *Gulaphallus falcifer* (p. 274)

CLASSIFICATION OF PHALLOSTETHIDAE

The following classification of phallostethids reflects some conclusions of the Phylogenetic Analysis. All higher taxa are monophyletic. Species are listed in order of year of description.

Family Phallostethidae Regan, 1913

Subfamily Phallostethinae Regan, 1913

Tribe Phallostethini new status

Genus *Phallostethus* Regan, 1913

P. dunckeri Regan, 1913

Genus *Phenacostethus* Myers, 1928*P. smithi* Myers, 1928*P. posthon* Roberts, 1971*P. trewavasae* Parenti, 1986

Tribe Neostethini new status

Genus *Neostethus* Regan, 1916*N. lankesteri* Regan, 1916*N. bicornis* Regan, 1916*N. palawanensis* (Myers, 1935), new combination*N. amaricola* (Villadolid and Manacop, 1935)*N. thessa* (Aurich, 1937), new combination*N. ctenophorus* (Aurich, 1937), new combination*N. borneensis* Herre, 1939*N. villadolidi* Herre, 1942*N. zamboangae* Herre, 1942*N. robertsi* new species

Subfamily Gulaphallinae Aurich, 1937

Tribe Gulaphallini new status

Genus *Gulaphallus* Herre, 1925*G. eximius* Herre, 1925*G. mirabilis* Herre, 1925*G. bikolanus* (Herre, 1926), new combination*G. falcifer* Manacop, 1936*G. panayensis* (Herre, 1942), new combination

SYSTEMATIC ACCOUNTS

Family Phallostethidae Regan, 1913

Type genus *Phallostethus* Regan, 1913

Phallostethinae Regan, 1913 (as subfamily of Cyprinodontidae)

Neostethinae Aurich, 1937 (as subfamily of Phallostethidae, type genus *Neostethus* Regan)Gulaphallinae Aurich, 1937 (misprinted Gulaphalinae, as subfamily of Phallostethidae, type genus *Gulaphallus* Herre)

DIAGNOSIS.—Small to minute, laterally compressed, nearly transparent, atherinomorph fishes, largest size recorded 37 mm SL. Anus and urogenital openings anterior, below pectoral fin base, in both sexes. A median, abdominal, slightly frayed, fleshy ridge or keel from urogenital openings to anterior rays of anal fin. First dorsal fin with one or two short spines or thickened rays, or no rays but pterygiophore may be present.

Copulatory organ of males a priapium. The following characters are of males, unless other-

wise noted. Main bony priapial support the proctal axial bone. Main externalized bone(s) a toxactinium, a toxactinium and a ctenactinium, or one or two ctenactinia. Anterior ramus of cleithrum elongate anteriorly or not. Postcleithra absent or present as small slivers of bone in both sexes. First pair of pleural ribs expanded anteroposteriorly and dorsoventrally, ventral tips meeting and enclosed in block of cartilage and/or bone, the antepleural element. Large, fibrous pad, the pulvinulus, if present, covers point of articulation of toxactinium, proctal axial bone, and anterior extent of cleithra. Fertilization internal, sperm bundles passed to females through seminal papilla, which may be large or small, smooth or ruffled, and supported internally by papillary and penial bones. Development oviparous; females lay fertilized eggs.

Males bilaterally asymmetric: anus and seminal papilla offset to opposite sides of body, proctal and aoproctal, respectively. Prominent externalized priapial bones arise on left or right side of body. Proctal, or proctal and aoproctal, transverse processes of fourth vertebrae expanded and oriented anteriorly or not. Females bilaterally symmetric except those of *Gulaphallus falcifer*, in which one pelvic ray is enlarged on either left or right side of body at urogenital openings. Pelvics otherwise absent or represented by bundle of fin rays, called fringe, surrounding epididymis. Small postanal papillae may contain rudimentary pelvic girdles and rays in adult female *Phenacostethus posthon* and *Gulaphallus eximius*.

Hyobranchial apparatus with reductions from typical atherinoid condition; teeth on fourth ceratobranchial toothplate present or absent. Branchiostegal rays 4 to 6.

DESCRIPTION.—Background uniformly pale yellow or straw-colored in alcohol, with small, dark melanophores on dorsal surface of head and body, midlateral intermuscular septum, along anal fin base, dorsal and ventral midline. Seminal papilla and externalized bones of priapium may be covered with scattered melanophores. Scales cycloid, relatively small to medium-sized, and deciduous. Dorsal scales with faint dark margins. Eye-lens large to minute. Dorsal surface of head with translucent, membranous dome or not. Mouth slightly to highly protractile with thin or no meniscus, cartilaginous rod, or ossified submaxillary element between maxilla and vomer. Unicuspid teeth in single or double row, with large teeth on lateral ramus of premaxilla, or few,

small teeth. Second dorsal fin with 5–10 rays. Anal fin unmodified, with 13–28 rays. Pectoral fin with 9–13 rays. Caudal fin emarginate, forming incipient lobes. Caudal skeleton with two epurals, autogenous parhypural, and dorsal and ventral hypural plate. Vertebrae 31–40.

REMARKS.—Regan (1913, 1916), Myers (1928), Bailey (1936), Herre (1942), and Roberts (1971b) listed both diagnostic and descriptive characters of phallostethid fishes. This diagnosis, like the ones that follow, is phylogenetic, as in Weitzman and Fink (1985) for genera of xenurobryconin characid fishes. Only characters or character states hypothesized to be derived are considered diagnostic of taxa. Comparisons among characters used to diagnose species, tribes, and subfamilies are given in the Phylogenetic Analysis and differential diagnoses.

Subfamily Phallostethinae Regan

DIAGNOSIS.—Priapium with a reduced second ctenactinium, and a prominent, shieldlike pulvinulus covering articulation point of robust toxactinium and proctal axial bone. Jaws of males and females highly protrusible with elongate premaxillary ascending processes and distinct submaxillary cartilages or bones, and a reduced hyobranchial apparatus with few or no teeth on fourth ceratobranchial toothplate.

COMPOSITION.—Two tribes, Phallostethini and Neostethini, both family-group names used for the first time at the tribal level.

Tribe Phallostethini new status

DIAGNOSIS.—Males with a large, fleshy seminal papilla that may be smooth or ruffled; toxactinium relatively straight to curved. Adults of both sexes extremely small and delicate, with deciduous scales; a translucent, membranous dome on dorsal surface of head.

COMPOSITION AND DISTRIBUTION.—Two genera, *Phallostethus* Regan from coastal peninsular Malaysia, and *Phenacostethus* Myers, from coastal peninsular Thailand and Malaysia and Sarawak, as diagnosed below.

Genus *Phallostethus* Regan, 1913

Phallostethus Regan, 1913:548–549 (type species: *Phallostethus dunckeri* Regan, 1913 by monotypy).

DIAGNOSIS.—As for *P. dunckeri* Regan, 1913, below.

COMPOSITION AND DISTRIBUTION.—One species from brackish water, mouth of Muar R., Johore, Malaysia (see Roberts 1971a:fig. 1).

Phallostethus dunckeri Regan, 1913

(Fig. 1)

Phallostethus dunckeri Regan, 1913:548–555, figs. 1–4 (original description, mouth of Muar R., Johore, Malay Peninsula); 1916:1, 16–25, figs. 12a, 13–15, pls. 1a, 11a, 1Va, b (characters, comparison with *Neostethus*). Myers 1928:1–6 (characters, comparison with *Phenacostethus*); 1937:137 (characters). Herre 1939:140 (characters). Roberts 1971a:1–20 (relationships). Parenti 1984:1–12, figs. 1–4 (osteology, relationships); 1986a:229–235, tables 1, 2 (relationships, characters); 1986c:41 (characters).

DIFFERENTIAL DIAGNOSIS.—*Phallostethus dunckeri* has an anal fin longer (26–28 rays, as opposed to 13–22) and vertebral number higher (40, as opposed to 31–37) than any other phallostethid. Males are readily separable from those of *Phenacostethus* by a serrated second ctenactinium. Both sexes distinct from *Phenacostethus* by lacking first dorsal fin, and a second dorsal fin with 8–10 rays, rather than 5–7.

MATERIAL.—Lectotype (designated by Ladiges et al. 1958): ZMH 193, dextral ♂, mouth of Muar R., Johore, Malaysia, 1902, G. Duncker, coll. Paralectotypes: BMNH 1913.5.24:18–22 (5 spec.: 1 sinistral ♂, 3 ♀, 1 sex undet.) and ZMH 194–195 (19 spec.: 2 dextral ♂, 14 ♀, 3 juv.), collected with lectotype.

REMARKS.—Ladiges et al. (1958) gave lectotype and paratype (=paralectotype) status to ZMH 193 and 194, respectively. Because ZMH 195 and the BMNH specimens are of the original syntypic series, they are also paralectotypes. Parenti (1986a) called all these specimens syntypes.

Genus *Phenacostethus* Myers, 1928

Phenacostethus Myers, 1928:6 (type species: *Phenacostethus smithi* Myers, 1928 by original designation).

DIFFERENTIAL DIAGNOSIS.—A lower jaw protruding beyond upper jaw and greatly reduced second ctenactinium distinguishes *Phenacostethus* from all other phallostethids. Anal and second dorsal fin rays and vertebrae are fewer than in *Phallostethus*. First dorsal fin with one ray as opposed to first dorsal fin absent in *Phallostethus*.

COMPOSITION AND DISTRIBUTION.—*Phenacostethus smithi* Myers, 1928 and *P. posthon* Roberts, 1971a, in fresh and brackish waters, Thailand and peninsular Malaysia; and *P. trewavasae* Parenti, 1986a, in freshwater, Sarawak, Malaysian Borneo.

Phenacostethus smithi Myers, 1928

(Figs. 1, 2)

Neostethus lankesteri (non Regan). Smith 1927:353–355 (report of specimens from Bangkok, Thailand).

Phenacostethus smithi Myers, 1928:6–8, figs. 1, 2 (original description, Bangkok, Thailand). Smith 1929:14 (characters, distribution). Myers 1937:137–138 (characters). Bailey 1936:470–474, pls. 3, 4 (anatomy, comparison with *Gulaphallus*). TeWinkel 1939:60–68, figs. 1–5 (anatomy, comparison with *Gulaphallus*). Herre 1939:140, 142 (characters, listed). Hubbs 1944:73 (characters). Smith 1945:475–476 (ecology). Roberts 1971a:4–18, figs. 1, 2, 4, 7 (mislabelled as fig. 6) (anatomy, relationships). Parenti 1986a:229–234, fig. 4a, tables 1, 2 (characters, relationships).

Phenacostethus thai Fowler, 1937:219–220, figs. 189, 190 (original description, Bangkok, Thailand).

DIFFERENTIAL DIAGNOSIS.—Unlike other phallostethins, males of *Phenacostethus smithi* have a ruffled, rather than smooth, distal end of enlarged seminal papilla.

MATERIAL.—Holotype: AMNH 9247, dextral ♂, 13.5 mm SL, Bangkok, Thailand, Dec. 1926, H. M. Smith, coll. Paratypes: AMNH 9248 (1 ♀, USNM 92979 (11 spec.: 4 sinistral ♂, 1 dextral ♂, 5 ♀, 1 sex undet.), USNM 202564 (1 ♀, USNM 104417 (1 sinistral ♂), CAS-SU 26520 (8 spec.: 2 sinistral ♂, 3 dextral ♂, 2 ♀, 1 juv.), ANSP 108764 (ex. SU 26520) (2 spec.: 1 dextral ♂, 1 ♀) and USNM 92297 (2 spec.: 1 dextral ♂, 1 ♀), collected with holotype.

Holotype and paratypes of *Phenacostethus thai*: ANSP 51352, ANSP 51353–60 (9 spec.: 2 sinistral ♂, 2 dextral ♂, 5 ♀), Bangkok, Thailand, 2 Aug. 1923, H. M. Smith, coll.

OTHER MATERIAL.—THAILAND: UMMZ 87345 (40 spec.: 10 sinistral ♂, 14 dextral ♂, 15 ♀, 1 juv.), MCZ 47055 (13 spec.: 6 sinistral ♂, 2 dextral ♂, 5 ♀), USNM 93506 (100+), USNM 93507 (50+), USNM 93508 (36 spec.: 5 sinistral ♂, 12 dextral ♂, 17 ♀, 2 juv.), USNM 88668 (100+), USNM 88667 (100+ spec.; 4 juv. cleared and stained), USNM 88659 (3 spec.: 1 sinistral ♂, 1 dextral ♂, 1 ♀), BMNH 1927.12.29:1–10 (31 spec.: 6 sinistral ♂, 4 dextral ♂, 10 ♀, 11 juv.; 2 cleared and stained), ZMA 100.652 (35), and CAS-SU 35957 (112 spec.: 5 cleared and stained), Bangkok, and MCZ 47299 (18 spec.: 1 sinistral ♂, 1 dextral ♂ and 2 ♀ cleared and stained), Chantaburi City. MALAYSIA: USNM 266124 (50+), Trengganu; USNM 266125 (3 spec.: 1 sinistral ♂, 2 ♀), USNM 266126 (15 spec.: 3 sinistral ♂, 5 dextral ♂, 7 ♀), USNM 266127 (1 ♀), Johore.

REMARKS.—In the original description of *Phenacostethus smithi*, Myers (1928:8) stated that “. . . nineteen paratypes, 11 males and 8 females, are deposited in the American Museum of Natural History, the United States National Museum, and my own collection.” I assume that Myers’s “own collection” was deposited, in part, in the Stanford University (SU) collection, now CAS-SU 26520 and ANSP 108764. However, I have no reason to exclude any of the above USNM paratypes of *Phenacostethus smithi* from type status.

In his description of *Phenacostethus thai*, Fow-

lers (1937) did not separate what he called the holotype from other type specimens and I am unable to separate that specimen from the rest of the type material. See also Böhlke (1984:140).

DISTRIBUTION.—Coastal fresh and brackish waters, Thailand and peninsular Malaysia (Roberts 1971a:fig. 1).

Phenacostethus posthon Roberts, 1971

(Fig. 1)

Phenacostethus posthon Roberts, 1971a:12–17, figs. 3, 5, 6 (mislabelled as fig. 7) (original description, Pungah and Langu Town, Thailand). Parenti 1986a:225–235, fig. 5, tables 1, 2 (characters, relationships); 1986b:308–309, figs. 4, 5 (anatomy).

DIFFERENTIAL DIAGNOSIS.—*Phenacostethus posthon* is unique among phallostethins, having a first dorsal fin origin posterior to base of last anal fin ray rather than opposite midpoint of anal fin so that first and second dorsal fins are relatively close together. Males are dextral, as in *Gulaphallus eximius* and *G. bikolanus*, as opposed to sinistral, as in *P. trewavasae*, or sinistral or dextral, as in all other phallostethids.

MATERIAL.—Holotype, MCZ 47300, ♂, 16.7 mm SL, Khlong Kla Soh, about 15 km SW of Pungah Town, Pungah Prov., Thailand, 29 June 1970, T. R. Roberts, coll. Paratypes: MCZ 47301 (2 ♂ cleared and stained), MCZ 47301A (22 ♀), MCZ 47301B (32 ♂), same data as holotype, and MCZ 47302 (20), Khlong Langu at Langu Town, 48 km NW of Satul Town, Thailand, 26 June 1970, T. R. Roberts, coll.

OTHER MATERIAL.—MALAYSIA: USNM 229302 (182 spec.: 82 ♂, 77 ♀, 23 juv.; 6 cleared and stained), Muar R., Johore.

DISTRIBUTION.—Coastal fresh and brackish waters, Thailand and peninsular Malaysia (Roberts 1971a:fig. 1).

Phenacostethus trewavasae Parenti, 1986

(Fig. 1)

Phenacostethus trewavasae Parenti, 1986a:226–229, figs. 1–3, 4b, tables 1, 2 (original description, Baram R., Sarawak, Malaysian Borneo).

DIFFERENTIAL DIAGNOSIS.—*Phenacostethus trewavasae* is unique among phallostethids, having a minute eye-lens, and males sinistral rather than dextral, as in *P. posthon*, *Gulaphallus eximius* and *G. bikolanus*, or sinistral or dextral, as in all other phallostethids.

MATERIAL.—Holotype: ROM 41826, ♂, 14.1 mm SL, Sungei Kejin Tugang, tributary of Sungei Kejin, Baram R., Sarawak, Malaysia, 3 Aug. 1981, D. Watson, coll. Paratypes: ROM 44289 (19), ROM CS812 (3 spec.: 2 ♂, 1 ♀, cleared and stained), ROM 41827 (1), collected with holotype. ROM 41829 (1), ROM

41830 (13), CAS 55454 (5 spec.; 1 cleared and stained), BMNH 1984.7.12:1–5 (5), AMNH 55570 (5), USNM 267266 (5), Sungei Kejin, station at confluence of Kejin Tugang and Kejin R., Baram R., Sarawak, Malaysia, 11 Feb. 1980, D. Watson, coll.

OTHER MATERIAL.—MALAYSIA: ROM 41828 (11), ROM 44290 (29 spec.: 2 ♂ and 2 ♀ cleared and stained) and ROM 44291 (50), Sarawak.

DISTRIBUTION.—Tributaries of Baram R., Sarawak, Malaysian Borneo (Fig. 1).

Tribe Neostethini new status

DIAGNOSIS.—Priapium with an inner pulvinular bone, and thin bony projections numbering 80 or more on papillary bone.

Genus *Neostethus* Regan, 1916

Neostethus Regan, 1916:1, 2 (type species: *Neostethus lankesteri* Regan, 1916 by original designation, use of "gen. et sp. n." for one of two included new species).

Plectrostethus Myers, 1935:5 (type species: *Plectrostethus palawanensis* Myers, 1935, by original designation).

Ceratostethus Myers, 1937:141 (type species: *Neostethus bicornis* Regan, 1916, by original designation).

Solenophallus Aurich, 1937:264 (unavailable; no type species designated of the two treated under genus).

Ctenophallus Herre, 1939:144 (type species: *Solenophallus ctenophorus* Aurich, 1937, by original designation).

Sandakanus Herre, 1942:151 (type species: *Neostethus borneensis* Herre, 1939, by original designation, as a subgenus of *Neostethus* Regan).

Solenophallus Herre (ex Aurich), 1953:242 (type species: *Solenophallus thessa* Aurich, 1937, by original designation).

DIAGNOSIS.—As for the tribe Neostethini, above.

COMPOSITION AND DISTRIBUTION.—Ten species: *N. lankesteri* Regan, 1916, Thailand, peninsular Malaysia, Singapore, and Borneo; *N. bicornis* Regan, 1916, peninsular Malaysia, Singapore, Thailand, Borneo, and Palawan, Philippines; *N. palawanensis* (Myers, 1935), Palawan, Philippines; *N. thessa* (Aurich, 1937), Mindanao, Philippines; *N. ctenophorus* (Aurich, 1937), Luzon, Philippines; *N. borneensis* Herre, 1939, Borneo and Coron, Philippines; *N. zamboangae* Herre, 1942, Mindanao and Luzon, Philippines; *N. robertsi* new species, Luzon, Philippines; *N. amaricola* (Villadolid and Manacop, 1935), and *N. villadolidi* Herre, 1942, throughout Philippines.

Neostethus lankesteri Regan, 1916

(Figs. 1, 3, 10c)

Neostethus lankesteri Regan, 1916:2–14, figs. 1–10, 12B, pls. 1B, 2, 3A, 4C (original description, Muar R., Johore, peninsular Malaysia, and Singapore). Weber and DeBeaufort

1922:381–383, fig. 103 (characters). Myers 1928:8 (characters). Smith 1929:13 (distribution). Myers 1937:139 (listed). Herre 1939:143 (listed). Roberts 1971a:8 (characters). Ivantsoff et al. 1987:651–652, figs. 2A–C, 3A (anatomy, comparisons with atherinoids).

Neostethus siamensis Myers, 1937:139–140 (original description, Chantabun R., Thailand). Herre 1939:143 (listed). Smith 1945:477 (compiled). Roberts 1971a:2–3 (collection report). Parenti 1986c:39–41, fig. 1 (osteology, histology).

Neostethus (*Neostethus*) *lankesteri*. Herre 1942:149 (characters, relationships, distribution).

Neostethus (*Neostethus*) *siamensis*. Herre 1942:150 (characters, probable synonym of *N. lankesteri* Regan).

DIFFERENTIAL DIAGNOSIS.—*Neostethus lankesteri* males can be recognized by a small, slightly pointed, triangular, ventral bony projection on elongate first ctenactinium, and posterior tips of first pleural ribs projecting beyond body of priapium. Females are unique among phallostethids having a large, hooklike, posteriorly projecting, urogenital papilla.

MATERIAL.—Lectotype (here designated): BMNH 1937.12.9:7, dextral ♂, 26.0 mm SL, Muar R., peninsular Malaysia, 18 Feb. 1902, G. Duncker, coll. Paralectotypes: BMNH 1937.12.9:8–10 (3 spec.: 1 dextral ♂, 1 sinistral ♂, 1 ♀) Singapore, G. Duncker, coll. Holotype of *Neostethus siamensis*: USNM 102140, adult ♀, 28.7 mm SL, Chantabun R., Thailand, Apr. 1933, H. M. Smith, coll.

OTHER MATERIAL.—SINGAPORE: BMNH 1970.7.22:71–77 (7 spec.: 1 sinistral ♂, 1 dextral ♂, 5 ♀), R. Tengah; BMNH 1970.7.22:78–79 (2 ♀), R. Serangoon; RMNH 26425 (69 spec.: 22 sinistral ♂, 29 dextral ♂, 18 ♀), R. Berih; CAS-SU 67162 (105 spec.: 5 cleared and stained), R. Selatar. MALAYSIA: FMNH 51653 (1 dextral ♂), East Coast Residency, CAS-SU 61762 (10 spec.: 6 sinistral ♂, 2 dextral ♂, 2 ♀), Sarawak. BRUNEI: CAS-SU 61763 (1). INDONESIA: AMS I.19355–041 (26 spec.: 7 sinistral ♂, 7 dextral ♂, 9 ♀, 3 juv.), East Kalimantan. THAILAND: MCZ 76857 (375 spec.: 6 cleared and stained), near Tha Chalap on road to Chantaburi, Chantaburi Prov.; MCZ 47200 (3), Satul Prov., CAS 63194 (2), Rayong Prov.; CAS 63195 (17), Chumphorn Prov.

DISTRIBUTION.—Coastal localities of Thailand, peninsular Malaysia, Singapore, and Borneo.

Neostethus bicornis Regan, 1916

(Figs. 1, 10d)

Neostethus bicornis Regan, 1916:14–16, fig. 11 (original description, Kuala Langat, peninsular Malaysia). Myers 1928:9 (characters). Herre and Myers 1937:70 (ecology, distribution).

Ceratostethus bicornis (Regan). Myers 1937:141–142 (relationships, referral to new genus). Herre 1939:142 (distribution); 1942:145 (characters, relationships, distribution); 1953:240 (synonymy, distribution). Roberts 1971a:6–10 (characters). Roberts 1971b:397–409, figs. 2–12 (osteology, functional anatomy). Rosen and Parenti 1981:20, fig. 19A (dorsal gill arch anatomy).

DIFFERENTIAL DIAGNOSIS.—Mature males have two elongate ctenactinia rather than a long first ctenactinium and short second ctenactinium as in other *Neostethus*. Immature males have a brown blotch on proctal pelvic fin rays that fades with growth and maturity. Females have a fleshy, hoodlike flap that covers urogenital openings.

MATERIAL.—Lectotype (here designated): BMNH 1937.12.9: 4, immature sinistral ♂, 20.9 mm SL, Kuala Langat, peninsular Malaysia, G. Duncker, coll. Paralectotypes: BMNH 1937.12.9: 5–6 (2 ♀, 16.7–19.1 mm SL), collected with lectotype.

OTHER MATERIAL.—THAILAND: MCZ 47304 (142 spec.; 2 ♀ cleared and stained); MCZ 76856 (71 spec.; 1 sinistral ♂ cleared and stained); MCZ 47305 (93 spec.; 1 dextral ♂ cleared and stained); MCZ 52364 (100+); MCZ 47306 (85 spec.; 1 dextral ♂ and 1 ♀ cleared and stained); MCZ 60081 (70), near Tha Chalap on road to Chantaburi, Chantaburi Prov.; CAS 63196 (2), Chumporn Prov. SINGAPORE: BMNH 1970.7.22: 69–70 (2 spec.: 1 dextral ♂, 1 ♀), R. Poyen; BMNH 1970.7.22: 63–68 (6 spec.: 3 dextral ♂, 3 ♀), R. Tengah; CAS-SU 67161 (10 spec.: 4 sinistral ♂, 5 dextral ♂, 1 juv.), R. Seletar; CAS-SU 35783 (51 spec.; 10 cleared and stained); MNHN 38-14 (4), R. Kranji; CAS-SU 31133 (11 spec.: 9 sinistral ♂, 1 dextral ♂, 1 ♀); USNM 102142 (8 spec.: 1 sinistral ♂, 4 dextral ♂, 3 ♀). BRUNEI: CAS-SU 61764 (1). MALAYSIA: USNM 189012 (5), mangrove swamps on island opposite Sandakan; FMNH 51726–51729 (173), East Coast Residency, Kinabatangan Dist.; and private collection of Maurice Kottelat (5), Sungei Seburut near Matang, Sarawak. PHILIPPINES: USNM 98839 (3) and USNM 150632 (2), Nakoda Bay; USNM 98840 (1), Malam-paya R.; USNM 98838 (3), Palawan. No locality: MCZ 60049 (50+).

DISTRIBUTION.—One of the most widespread phallostethids; coastal localities of Thailand, peninsular Malaysia, Singapore, Borneo, and Palawan, Philippines.

Neostethus amaricola

(Villadolid and Manacop, 1935)

(Figs. 1, 9b)

Gulaphallus amaricola Villadolid and Manacop, 1935:194–196, pl. 1 (original description, Pasay, Rizal Prov., Luzon, Philippines).

Neostethus amaricola (Villadolid and Manacop). Myers 1937: 139 (characters, referral of *G. amaricola* to *Neostethus*). Herre 1939:143 (distribution). Hubbs 1944:73–74 (characters). Herre 1953:241 (distribution).

Neostethus (*Neostethus*) *amaricola*. Herre 1942:149 (characters, relationships, distribution).

DIFFERENTIAL DIAGNOSIS.—Distal tips of first pleural ribs of females of *Neostethus amaricola* project beyond ventral body profile. Males may be recognized by a sharply pointed second ctenactinium directly anteriorly, rather than dorsally as in *N. villadolidi*.

MATERIAL.—PHILIPPINES: USNM 98835 (6 spec.: 1 sinistral ♂, 5 ♀; 13–20 mm SL), Ragay R., Ragay Gulf; FMNH 40771–40785 (15 spec.: 2 sinistral ♂, 5 dextral ♂, 6 ♀, 2 juv.; 13–21 mm SL), Navotas; CAS-SU 32354 (3 spec.: 2 sinistral ♂, 1 ♀; 20–23 mm SL), Nasugbu; CAS-SU 32926 (6 spec.: 1 sinistral ♂, 2 dextral ♂, 3 ♀; 23–24 mm SL), Manila; USNM 98834 (2 spec.: 1 sinistral ♂, 1 dextral ♂), Port San Vicente; USNM 98833 (3 sinistral ♂), Manila Bay; CAS-SU 38898 (200+ spec.; 13 cleared and stained), Navotas; CAS 50724 (266), Nipa creek S. of Masinloc, Luzon. CAS-SU 38899 (190 spec.; 5 cleared and stained), Mindoro.

In the original description, Villadolid and Manacop (1935:195) stated that there were to be at least one male and one female, as well as several additional cotypes collected in Pasay, Rizal Prov., Luzon, in the zoological museum of the College of Agriculture, University of the Philippines. These specimens are presumed lost.

DISTRIBUTION AND REMARKS.—A *Neostethus* species widespread in coastal, brackish-water habitats throughout the Philippines, including Luzon and Mindoro. Herre (1942, 1953) reported *N. amaricola* from Leyte; however, I have reidentified two USNM lots from that locality as the closely related *N. villadolidi*.

Neostethus borneensis Herre, 1939

(Fig. 1)

Neostethus borneensis Herre, 1939:143 (original description, report from around Sandakan Bay, North Borneo); 1940b: 14–17, pls. 10, 11 (description, Kabili R., Sandakan Bay, Segaliud R., North Borneo).

Neostethus (*Sandakanus*) *borneensis*. Herre 1942:151–152 (characters, relationships, distribution); 1953:242 (listed as type species of subgenus *Sandakanus*).

Neostethus (*Sandakanus*) *coronensis* Herre, 1942:152–153 (original description, Coron, Busuanga, Philippines); 1953: 242 (distribution).

Böhlke (1953) followed Herre (1942) in treating Herre's (1940b:14–17) detailed discussion, which included the heading "*Neostethus borneensis*, new species," as the original description. However, Herre's 1940b publication was predated by a compilation and brief statement of identifying characters of phallostethid species (Herre 1939), in which the name, characters, and statement of distribution are recorded. This constitutes the original description of *N. borneensis*.

DIFFERENTIAL DIAGNOSIS.—*Neostethus borneensis* is a robust, relatively short-bodied species with vertebrae (31–32, as opposed to 34–37), and scales in a lateral series (25–27, as opposed to 29–34), fewer than in congeners.

MATERIAL.—Holotype: CAS-SU 33018, sinistral ♂, 16.5 mm SL, Kabili R., Sandakan Dist., North Borneo, 30 Jan. 1937, A. W. C. T. Herre, coll. Paratypes: CAS-SU 33022 (116 ♂; 2 cleared and stained), CAS-SU 33019 (45 ♀), FMNH 51537–51538 (12 spec.: 6 ♂ and 6 ♀). BMNH 1938.12.1:155–164 (19 spec.: 8 ♂, 3 ♀, 8 juv.), collected with holotype. CAS-SU 69021 (7), CAS-SU 69022 (6 cleared and stained), CAS-SU 33020 (9) Segaliud R., North (Malaysian) Borneo, A. W. C. T. Herre, coll. Holotype of *Neostethus coronensis*: CAS-SU 36542, dextral ♂, 22.5 mm SL, Coron, Busuanga, Philippines, 28 June 1940, A. W. C. T. Herre, coll. Paratypes of *N. coronensis*: CAS-SU 36543 (109 spec.: 23 sinistral ♂, 25 dextral ♂, 52 ♀, 9 juv.; 3 cleared and stained) collected with holotype.

OTHER MATERIAL.—MALAYSIA: FMNH 51654 (16), East Coast Residency; USNM 189015 (23), mangrove swamps on island opposite Sandakan.

DISTRIBUTION.—Borneo and Coron, Busuanga, Philippines.

Neostethus villadolidi Herre, 1942

(Figs. 1, 9a, 10b)

Neostethus (Neostethus) villadolidi Herre, 1942:150 (original description, Misamis Oriental, Mindanao, and Negros Oriental, Philippines).

Neostethus villadolidi. Herre 1953:241–242 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Neostethus villadolidi* is a slender-bodied species closely allied with *N. amaricola*, but differing from it and all other phallostethids by having a sharply pointed, dorsally directed, second ctenactinium, and a fleshy urogenital protuberance in females.

MATERIAL.—Holotype: CAS-SU 36537 (misprinted 23637 in original description), sinistral ♂, 22.5 mm SL, mangrove swamp next to Fishery Experiment Station, Cagayan de Misamis, Misamis Oriental Prov., Mindanao, Philippines, 20 Aug. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36538 (59 spec.: 14 sinistral ♂, 13 dextral ♂, 26 ♀, 6 juv.), collected with holotype.

OTHER MATERIAL.—PHILIPPINES: CAS-SU 52344 (36 spec.: 4 cleared and stained), CAS-SU 36566 (19 spec.: 2 sinistral ♂, dextral ♂, 11 ♀, 5 juv.), and CAS-SU 32355 (111 spec.: 5 sinistral ♂, 31 dextral ♂, 58 ♀, 17 juv.; 7 cleared and stained), CAS 60258 (20 spec.: 10 ♂ and 10 ♀), MNHN 38-15 (4), ROM 54986 (158), ROM 54987 (13), ROM 54988 (80), ROM 50489 (1), ROM 51854 (426), Negros Oriental; AMS I.21938-016 (39), Mactan Island, Cebu; CAS 54645 (12 spec.: 6 dextral ♂, 5 ♀, 1 juv.), northern end of Cuyo, Palawan Prov.; USNM 98836 (1 ♀, 21 mm SL), USNM 98837 (2 spec.: 1 ♀ and 1 dextral ♂), Leyte.

Herre (1942:150) mentioned two lots from Negros Oriental without catalogue numbers, questionably to be included in the description of *N. villadolidi*. I list here several lots from Negros Oriental; however, like Böhlke (1953), I recognize none as type material.

DISTRIBUTION.—Mindanao, Cuyo, Mactan, Negros Oriental and Leyte, Philippines.

Neostethus zamboangae Herre, 1942

(Fig. 1)

Neostethus (Sandakanus) zamboangae Herre, 1942:153–154 (original description, Zamboanga, Mindanao, Philippines); 1953:242 (distribution).

DIFFERENTIAL DIAGNOSIS.—Males of *Neostethus zamboangae* are readily distinguished from congeners by two prominent ctenactinia: an elongate first ctenactinium, and a smaller, hooked second ctenactinium with from two to seven bony serrations. *Phallostethus dunckeri* males also have a serrated second ctenactinium; however, numerous derived characters that distinguish phallostethins from neostethins support a conclusion that these similar second ctenactinia are independently derived.

MATERIAL.—Holotype: CAS-SU 36544, dextral ♂, 22 mm SL, Zamboanga, Mindanao, Philippines, 6 Sep. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36545 (242 spec.: 30 sinistral ♂, 45 dextral ♂, 117 ♀, 50 juv.; 4 cleared and stained) collected with holotype.

OTHER MATERIAL.—PHILIPPINES: CAS 50725 (141 spec.: 4 cleared and stained); UMMZ 211666 (37), Sorsogon Bay, Buhatan R., 5 km E of Sorsogon Town, Luzon.

DISTRIBUTION.—Coastal localities of Zamboanga, Mindanao and Sorsogon, Luzon, Philippines.

Neostethus palawanensis (Myers, 1935), new combination

(Fig. 1)

Plectrosethust palawanensis Myers, 1935:5–6 (original description, mouth of the Caiholo R., Ulugan Bay, west coast of Palawan, Philippines). Myers 1937:141 (characters). Herre 1939:144 (distribution); 1942:155 (characters, relationships, distribution). Hubbs 1944:71, 73 (characters). Herre 1953:242 (distribution).

Plectrosethust palawensis (misspelling of *P. palawanensis* Myers). Ivantsoff et al. 1987:653–654, fig. 41 (anatomy, comparisons with atherinoids).

DIFFERENTIAL DIAGNOSIS.—*Neostethus palawanensis* is a slender-bodied species readily distinguished by a relatively straight first ctenactinium with a broad, fleshy ventral ridge.

MATERIAL.—Holotype: USNM 93421, sinistral ♂, 22.5 mm SL, mouth of Caiholo R., Ulugan Bay, west coast of Palawan, Palawan Prov., Philippines, 29 Dec. 1908, U.S.S. "Albatross." Paratypes: USNM 93422 (♀, 19 mm SL, allotype = paratype); USNM 93423 (8 spec.: 5 dextral ♂, 3 ♀), collected with holotype.

OTHER MATERIAL.—PHILIPPINES: USNM 93424 (eggs only) collected with holotype and paratypes (no type status). CAS 63200 (17 spec.: 5 sinistral ♂, 4 dextral ♂, 8 ♀; 4 cleared and stained), Cuyo, Palawan Prov.

DISTRIBUTION.—Coastal localities of Palawan and Cuyo, Palawan Prov., Philippines.

Neostethus thessa (Aurich, 1937),
new combination
(Figs. 1, 10a)

Solenophallus thessa Aurich, 1937:264–272, table 1, figs. 1A, 3–5, 7I (original description, Lake Mainit, Mindanao, Philippines). Herre 1939:142 (distribution); 1953:242 (valid description of *Solenophallus*).

DIFFERENTIAL DIAGNOSIS.—*Neostethus thessa* is readily distinguished from congeners by: no dorsal fin rays (remnant of first dorsal pterygiophore present in some specimens); oral dentition reduced to several small, unicuspid teeth on premaxilla and dentary; anal fin with 17–22 rays, as opposed to 13–18; and second dorsal fin with 8–10 rays, as opposed to 5–7.

MATERIAL.—PHILIPPINES: CAS-SU 36546 (46 spec.: 9 sinistral ♂, 9 dextral ♂, 26 ♀, 2 juv.; 9 cleared and stained), Lake Mainit, Mindanao (type locality, no type status).

This is the only known material of *N. thessa*. Aurich (1937) indicated that he based his original description on at least one male (26 mm SL) and one female (29 mm SL), without giving place of deposition of any type or other material. No specimens of *Neostethus thessa* are present in collections of the ZMB (H. J. Paepke, pers. comm.) and ZMH (H. Wilkens, pers. comm.). However, I do not designate a neotype from the CAS-SU material, even though it is from the type locality, because Aurich's material may eventually be located upon a thorough search of possible collections, and, to my knowledge, there has never been confusion or concern among ichthyologists over identification of the species associated with the name *Solenophallus thessa* Aurich.

DISTRIBUTION.—Lake Mainit, Mindanao, Philippines (Fig. 1).

Neostethus ctenophorus (Aurich, 1937),
new combination
(Fig. 1)

Solenophallus ctenophorus Aurich, 1937:272–275, table 1, figs. 6, 7II–V (original description, Laguna de Bay, Luzon, Philippines).

Ctenophallus ctenophorus (Aurich). Herre 1939:144 (referral

to new genus); 1942:154–155 (characters, distribution, relationships); 1953:240 (synonymy).

REMARKS.—Herre (1942:154) diagnosed *Ctenophallus* as distinct “. . . from other phallos-tethids by the presence of a dense fringe along both margins of the open groove on the priapium.” This statement was extracted from Aurich's (1937) original description based on at least one male (24 mm SL) and one female (20 mm SL). Place of deposition of type or other material was not given by Aurich. No specimens of *N. ctenophorus* are present in collections of the ZMB (H. J. Paepke, pers. comm.) or the ZMH (H. Wilkens, pers. comm.).

The “dense fringe” is formed by the numerous bony projections of the papillary bone, diagnostic of *Neostethus*. The same character was also used by Myers (1935) to diagnose his new genus, *Plectrostethus*, literally a “quill on the chest,” placed here in synonymy of *Neostethus*.

I have examined no specimens of *N. ctenophorus*; however, without this species, the genus *Neostethus* is paraphyletic. Therefore, I synonymize *Ctenophallus* with *Neostethus*. Meristic data summarized in Table 2 are from Aurich (1937).

DISTRIBUTION.—Laguna de Bay, Luzon, Philippines.

Neostethus robertsi new species

(Figs. 1, 12, 13)

HOLOTYPE.—CAS 50723, dextral ♂, 22.3 mm SL, Calasiao R., about 12 km N of San Carlos City, Pangasinan Prov., Luzon, Philippines, 16 Mar. 1976, T. R. Roberts, coll.

PARATYPES.—CAS 64254 (40 spec.: 12 sinistral ♂, 9 dextral ♂, 10 ♀, 9 juv. or sex unde., 9.0–23.0 mm SL; 1 sinistral ♂, 1 dextral ♂ and 1 ♀ cleared and stained), collected with holotype.

DIFFERENTIAL DIAGNOSIS.—*Neostethus robertsi*, like *N. palawanensis*, has a second ctenactinium which is bifurcated distally, but distinguished from that species by having a larger, better-developed, claw-shaped second ctenactinium, and a slightly bowed second ctenactinium that lacks a fleshy, ventral ridge.

DESCRIPTION.—A small, laterally compressed species, largest size recorded 23.0 mm SL. No vestigial pelvic fin rays or bones in adult females; males with pelvic and parts of pectoral fin modified into priapium that is either dextral (holotype and eight ♂ paratypes) or sinistral (13 ♂ paratypes). Prominent externalized subcephalic bone a first ctenactinium, arising on either left or right

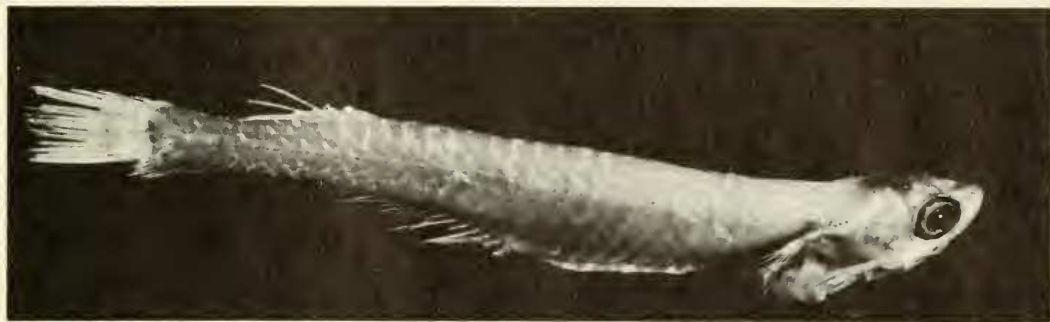


FIGURE 12. *Neostethus robertsi* new species. Holotype (CAS 50723), dextral male, 22.3 mm SL.

side of body and articulating with posterior extent of left or right (proctal) axial bone, curving gently along the left or right side of the head and the tip lying just ventral to lower jaw. First ctenactinium smooth, without fleshy, ventral ridge. Large, well-developed, claw-shaped second ctenactinium. Fibrous pulvinulus lateral to, and covering articulation point of, inner pulvinular and proctal axial bones. Pleural ribs of fourth vertebra in males expanded anteroposteriorly, their distal tips meeting on right side of proctal axial bone in sinistral males and left side in dextral males. First pleural rib on third vertebra in females.

Ventral dermal keel extending from posterior extent of priapium in males or urogenital opening in females, to anal fin origin. Scales on body of moderate size, deciduous. Color in alcohol like most other phallostethids: ground coloration very pale yellow or light brownish (straw-colored). Dark brown melanophores scattered on dorsal surface of head, along midlateral intermuscular septum, on operculum and priapium, and along basal portion of anal fin, dorsal and ventral midline. Dorsal scales with faint dark margins. Eyes large.

Skull and jaws like those illustrated for *Neostethus bicornis* by Roberts (1971b), with little modification. Jaw teeth small, conical, in a single uneven row or grouped together in indistinct rows.

Caudal skeleton with two epurals, autogenous parhypural, and a dorsal and a ventral hypural plate. Caudal fin rays broken in nearly all specimens examined. Pectoral fin narrow and elongate, with 10–11 rays. Two dorsal fins, the first with two spines or thickened rays supported by a single pterygiophore, the second with 6 rays. Anal fin rays 17–18, vertebrae 36, scales in a

lateral series 30, branchiostegal rays 5 (see Table 2).

DISTRIBUTION.—Pangasinan Prov., Luzon, Philippines (Fig. 1).

ETYMOLOGY.—The specific name, *robertsi*, in honor of Tyson R. Roberts, collector of the type series and student of phallostethid fishes.

Subfamily Gulaphallinae Aurich Tribe Gulaphallini new status

DIAGNOSIS.—Adult males with a perforated gular flap of skin through which anterior end of first ctenactinium projects and remains while at rest; and an aproctal axial bone that projects beyond ventral body profile with a small postero-dorsal crest.

Genus *Gulaphallus* Herre, 1925

Gulaphallus Herre, 1925:508 (type species: *Gulaphallus eximius* Herre, 1925, by subsequent designation of Myers 1928: 9).

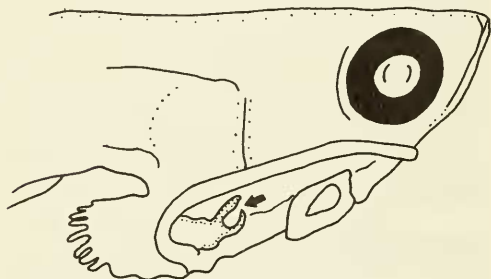


FIGURE 13. Diagrammatic representation of head and anterior portion of body, *Neostethus robertsi*, dextral male, CAS 50723. Anterior to the right. Arrow points to second ctenactinium.

Mirophallus Herre, 1926:539 (type species: *Mirophallus bikolanus* Herre, 1926, by monotypy).

Acanthostethus Herre, 1929:141–142 (type species: *Gulaphallus falcifer* Manacop, 1936, by original designation; preoccupied by *Acanthostethus* Smith, 1869 in Hymenoptera).

Manacopus Herre, 1940a:141 (replacement name for *Acanthostethus* Herre, 1939, and therefore taking same type species: *Gulaphallus falcifer* Manacop, 1936).

DIAGNOSIS.—As for the tribe *Gulaphallini*, above.

COMPOSITION AND DISTRIBUTION.—Five species, four from freshwater hill-streams, Luzon, *G. eximius* Herre, 1925, *G. mirabilis* Herre, 1925, *G. falcifer* Manacop, 1936, and *G. bikolanus* (Herre, 1926), and one from coastal brackish to marine localities, Panay, *G. panayensis* (Herre, 1942), Philippines.

Gulaphallus eximius Herre, 1925

(Fig. 1)

Gulaphallus eximius Herre, 1925:509–510, pls. 1, 2; figs. 1, 2 (original description, Nueva Vizcaya Province, Luzon, Philippines). Myers 1928:9 (characters). Herre 1939:142 (characters, distribution). Hubbs 1944:73 (characters). Herre 1953:241 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus eximius*, the largest phallostethid species, reaches 37 mm SL, and has more than 50 (range 52–58) scales in lateral series, as opposed to 25–38, in all other phallostethids. A brown blotch surrounds anus and urogenital openings in immature females. Rudimentary pelvic girdle represented by two small scale-shaped discs of bone in adult females. Males dextral as in *G. bikolanus*, but unlike that species, a first dorsal fin is present in both sexes.

MATERIAL.—Lectotype (designated by Böhlke 1953): CAS-SU 24474, ♂ 33.5 mm SL, creek, Santa Fe, Nueva Vizcaya Prov., Luzon, Philippines, 18 May 1924, R. C. McGregor, coll. Paralectotypes: CAS-SU 18149 (3 spec.: 1 ♂, 2 ♀), collected with lectotype.

OTHER MATERIAL.—PHILIPPINES: BMNH 1933.3.11.168 (1 ♂, 32.2 mm SL), FMNH 40593–40596 (4 spec.: 1 ♂, 2 ♀, 1 immature ♂), CAS-SU 38900 (72 spec.; 11 cleared and stained), CAS-SU 36832 (4 spec.: 1 ♂, 2 ♀, 1 juv.), Luzon.

DISTRIBUTION.—Mountain streams, Luzon, Philippines.

Gulaphallus mirabilis Herre, 1925

(Figs. 1, 4, 5)

Gulaphallus mirabilis Herre, 1925:511, pl. 2, figs. 3–5 (original description, Ibo creek, tributary of Angat R., Bulacan Province, Luzon, Philippines). Myers 1928:10 (characters). Villalolod and Manacop 1935:196–217, pls. 1–4, figs. 1–3 (anat-

omy, development). Bailey 1936:457–470, pls. 1, 2 (osteology). Aurich 1937:275–279, figs. 8, 9 (anatomy). Myers 1937:142 (characters). TeWinkel 1939:63–67 (anatomy, development). Herre 1939:142 (characters, distribution); 1942:144–145 (characters, distribution, relationships). Hubbs 1944:73 (characters). Herre 1953:241 (distribution). Roberts 1971b:411 (characters). Grier et al. 1980:332, table 1 (testis structure). Rosen and Parenti 1981:20, fig. 19B (dorsal gill arch anatomy).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus mirabilis* is readily distinguished from congeners by scales in lateral series ranging from 36 to 38 as opposed to from 28 to 32, or more than 50.

MATERIAL.—PHILIPPINES: Luzon: ANSP 91045 (4 spec.: dextral ♂, ♀, 2 juv., 12–25 mm SL), BMNH 1933.3.11.169–186 (18 spec.: 3 dextral ♂, 2 sinistral ♂, 11 ♀, 2 immature; 1 dextral ♂ and 1 ♀ cleared and stained), FMNH 76769 (6 spec.: 1 dextral ♂, 5 juv.), CAS 727 (1), CAS 728 (1), CAS 731–735 (5), CAS 740–743 (4), CAS 747–751 (5), CAS-SU 30720 (165), CAS-SU 38903 (64 spec.; 5 cleared and stained), CAS-SU 35959 (25), CAS 54938 (2 spec.: 1 sinistral ♂, 1 ♀), CAS-SU 35958 (121 spec.: 11 sinistral ♂, 15 dextral ♂, 32 ♀, 63 juv.), FMNH 46946 (9 spec.: dextral ♂, 4 ♀, 4 juv.), USNM 94293 (26 spec.: 8 dextral ♂, 4 ♀, 14 juv.), USNM 104412 (2), MCZ 33904 (10), MNHN 27-192, 193 (25, labelled syntypes, but not from type locality), MNHN 32-204 (4), ZMA 100.651 (4 spec.: 1 dextral ♂, 1 ♀, 2 juv., 17–29 mm SL), Molawin Creek, CAS-SU 38209 (1 ♀), CAS 50721 (279), UMMZ 211664 (54), Olo Creek, CAS-SU 38901 (7), CAS-SU 38902 (1 cleared and stained), Sison, and CAS 50719 (230), Barabac Creek, Pangasinan Prov.; CAS-SU 38904 (43 spec.: 4 sinistral ♂, 6 dextral ♂, 24 ♀, 9 juv., 13–31 mm SL; 2 dextral ♂ and 2 ♀ cleared and stained), FMNH 40623–40627 (4 spec.: 2 sinistral ♂, 2 ♀), Santa Maria R.; MCZ 33904 (10), Los Banos, Laguna Prov.; USNM 197728 (31 juv.). Central Luzon: CAS 50720 (23 spec.: 3 sinistral ♂, 2 dextral ♂, 8 ♀, 10 juv.), Porac R., Pampanga Prov.

DISTRIBUTION AND REMARKS.—One of the best-known and frequently collected phallostethid species because of its abundance in Molawin Creek, which flowed through the campus of the College of Agriculture, Luzon, Philippines (Herre 1942). Known also from other localities throughout Luzon.

Gulaphallus falcifer Manacop, 1936

(Fig. 1)

Gulaphallus falcifer Manacop, 1936:375–379, pls. 1, 2 (original description, Barrio Laput, Mexico, Pampanga Prov., and Nampicuan, Nueva Ecija, Luzon, Philippines).

Acanthostethus falcifer (Manacop). Herre 1939:141–143 (referral to new genus).

Manacopus falcifer (Manacop). Herre 1940a:141 (referral to new genus); 1942:146–147 (characters, distribution, relationships); 1953:241 (synonymy). Parenti 1986b:306–309, figs. 1–3 (anatomy, development).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus falcifer* is the only phallostethid species in which

females as well as males exhibit bilateral asymmetry: adult females with an elongate pelvic fin ray, on either left or right pelvic girdle, that projects beyond body profile to left or right of urogenital openings.

MATERIAL.—PHILIPPINES: Luzon: CAS-SU 32356 (42 spec.: 9 sinistral ♂, 14 dextral ♂, 10 sinistral ♀, 3 dextral ♀, 6 juv.; 7 cleared and stained), Barrio Laput, Pampanga Prov. (type locality). No locality: CAS 63198 (2 cleared and stained).

REMARKS.—Manacop (1936) lists the following type material: Holotype: Philippine Fish and Game Administration 31778, adult ♂, 27.5 mm SL, gourami pond at Barrio Laput, Mexico, Pampanga Prov., Luzon, Philippines, 27 Aug. 1935, C. Sandiko, coll. Allotype (=paratype): Philippine Fish and Game Administration 31779 (adult ♀ 26.5 mm SL). Paratypes: Philippine Fish and Game Administration 31780 (17 spec.: 8 ♀ and 9 ♂). This material is presumed unavailable for study. Böhlke (1953) did not designate a neotype from the CAS-SU material.

DISTRIBUTION.—Barrio Laput, Pampanga Prov., Luzon, Philippines.

Gulaphallus bikolanus (Herre, 1926),
new combination
(Fig. 1)

Mirophallus bikolanus Herre, 1926:540–541, pl. 3 (original description, Lake Bato, Camarines Sur Province, and Lake Lanigay, Albay Province, Luzon, Philippines). Myers 1928: 10–11 (characters). Aurich 1937:279–282, fig. 10 (anatomy). Myers 1937:142 (characters). Herre 1939:142 (distribution); 1942:142 (characters, distribution, relationships). Hubbs 1944:73–74 (characters). Herre 1953:241 (distribution). Parenti 1986a:234, table 2 (bilateral asymmetry).

DIFFERENTIAL DIAGNOSIS.—Males of *Gulaphallus bikolanus* are dextral as in *G. eximius*, but unlike that species, both males and females of *G. bikolanus* lack a first dorsal fin and have 32 scales in a lateral series, as opposed to more than 50.

MATERIAL AND REMARKS.—Lectotype (designated by Böhlke 1953). CAS-SU 24475, immature ♂, 19.5 mm SL, Lake Bato, Camarines Sur Prov., Luzon, Philippines, 30 Jan. 1926, G. A. Lopez, coll. Paralectotypes: CAS-SU 18148 (2 ♀, 22–23 mm SL), MNHN 27-194 (2, 21.1–23.8 mm SL), collected with lectotype. Böhlke (1953) was apparently unaware of the MNHN specimens, collected with the syntypes, which also have paralectotype status.

OTHER MATERIAL.—PHILIPPINES: AMNH 50592 (24 spec.: 13 dextral ♂, 9 ♀, 2 juv.), CAS 50722 (194 spec.: 131 dextral ♂, 55 ♀, 8 juv.), Guinobatan R., CAS 53165 (70 spec.: 24 dextral ♂, 37 ♀, 9 juv.), UMMZ 211665 (12 spec.: 5 dextral ♂, 7 ♀), Cabangan R., Albay Prov., Bikol Region, Luzon.

DISTRIBUTION.—Camarines Sur and Albay provinces, Luzon, Philippines.

Gulaphallus panayensis (Herre, 1942),
new combination
(Fig. 1)

Neostethus (Sandakanus) panayensis Herre, 1942:153 (original description, Capiz and Estancia, Panay, Philippines); 1953: 242 (distribution).

DIFFERENTIAL DIAGNOSIS.—*Gulaphallus panayensis* is a small, slender species known only from limited type material, with vertebrae 31–33, as opposed to 35–37, and scales in lateral series 28–30, as opposed to 32–58 in congeners. The largest male (holotype) does not have a completely developed priapium; however, I conclude, primarily from examination of cleared and stained specimens, that *panayensis* is a *Gulaphallus*.

MATERIAL.—Holotype: CAS-SU 36539, dextral ♂, 19.0 mm SL, Capiz, Panay, Philippines, 3 Aug. 1940, A. W. C. T. Herre, coll. Paratypes: CAS-SU 36540 (22 spec.: 1 sinistral ♂, 3 dextral ♂, 18 ♀; 2 cleared and stained) collected with holotype, and CAS-SU 36541 (22 spec.: 5 dextral ♂, 15 ♀, 2 juv.), Estancia, Panay, Philippines, 27 July 1940, A. W. C. T. Herre, coll.

DISTRIBUTION.—Capiz and Estancia, Panay, Philippines (Fig. 1).

CONCLUSIONS

1. The Phallostethidae comprise a monophyletic group of 19 species, classified in four genera, of three monophyletic tribes—Phallostethini, Neostethini, and Gulaphallini. Phallostethini (containing *Phallostethus* and *Phenacostethus*) and Neostethini (containing solely *Neostethus*) are sister taxa comprising the subfamily Phallostethinae. Subfamily Gulaphallinae is coextensive with tribe Gulaphallini and genus *Gulaphallus*.

2. Of the 19 recognized species, one, *Neostethus robertsi*, from Luzon, Philippines, is described as new. *Neostethus siamensis* Myers, 1937 is placed in synonymy of *Neostethus lankesteri* Regan, 1916; *Neostethus coronensis* Herre, 1942 is placed in synonymy of *Neostethus borneensis* Herre, 1939. Five new combinations are proposed: *Plectrostethus palawanensis* Myers, 1935, *Solenophallus thessa* Aurich, 1937 and *S. ctenophorus* Aurich, 1937, are placed in *Neostethus*; *Mirophallus bikolanus* Herre, 1926 and *Neoste-*

thus *panayensis* Herre, 1942 are placed in *Gulaphallus*.

3. All known names proposed for parts of the bilaterally asymmetric priapium are listed and defined; synonyms and presumed homologs are identified. Derived characters of the priapium provide the primary information for species group recognition. However, bilateral asymmetry in females of one species (*G. falcifer*), elaborate urogenital coverings in females of three species (*N. lankesteri*, *N. borneensis*, and *N. villadolidi*), and ontogenetic changes in pigmentation pattern of the anus and urogenital openings in females of one species (*Gulaphallus eximius*) indicate that the complex evolution of the male priapium has been paralleled by numerous modifications in the reproductive system of females.

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LITERATURE CITED

- AURICH, H. 1937. Die Phallostethiden (Unterordnung Phallostethoidea Myers). *Intl. Rev. Ges. Hydrobiol. Hydrogr.* 34:263-286.
- BAILEY, R. J. 1936. The osteology and relationships of the phallostethid fishes. *J. Morph.* 59:453-483.
- BÖHLKE, E. B. 1984. Catalog of type specimens in the ichthyological collection of the Academy of Natural Sciences of Philadelphia. *Acad. Nat. Sci. Philad., Spec. Publ.* 14:1-246.
- BÖHLKE, J. 1953. A catalogue of the type specimens of recent fishes in the Natural History Museum of Stanford University. *Stanford Ichthyol. Bull.* 5:1-168.
- COLLETTE, B. B., G. E. MCGOWEN, N. V. PARIN, AND S. MITO. 1984. Beloniformes: development and relationships. Pp. 334-354 in *Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. *Am. Soc. Ichthyol. Herpetol. Spec. Publ.* No. 1.
- DINGERKUS, G. AND L. D. UHLER. 1977. Enzyme clearing of alcian blue stained whole small vertebrates for demonstration of cartilage. *Stain Tech.* 52:229-232.
- DUNCKER, G. 1904. Die Fische der malayischen Halbinsel. *Mitt. Nat. Mus. Hamburg* 21:133-207.
- FOWLER, H. W. 1937. Zoological results of the third de-Schauensee Siamese Expedition, Part VIII—fishes obtained in 1936. *Proc. Philad. Acad. Nat. Sci.* 89:125-264.
- GRIER, H. J. AND B. B. COLLETTE. 1987. Unique spermatozeugmata in testes of halfbeaks of the genus *Zenarchopterus* (Teleostei: Hemiramphidae). *Copeia* 1987:300-311.
- GRIER, H. J., J. R. LINTON, J. F. LEATHERLAND, AND V. L. DE VLAMING. 1980. Structural evidence for two different testicular types in teleost fishes. *Am. J. Anat.* 159:331-345.
- HENNIG, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press, Urbana, Illinois. 263 pp.
- HERRE, A. W. C. T. 1925. Two strange new fishes from Luzon. *Philipp. J. Sci.* 27:507-513.
- . 1926. Four new Philippine fishes. *Philipp. J. Sci.* 31:533-543.
- . 1939. The genera of Phallostethidae. *Proc. Biol. Soc. Wash.* 52:139-144.
- . 1940a. *Manacopus*, a new name for a genus of Phallostethidae. *Copeia* 1940:141.
- . 1940b. New species of fishes from the Malay Peninsula and Borneo. *Bull. Raffles Mus.* 16:5-26.
- . 1942. New and little known phallostethids, with keys to the genera and Philippine species. *Stanford Ichthyol. Bull.* 2:137-156.
- . 1953. Check list of Philippine fishes. *U.S. Fish Wildl. Ser. Res. Rep.* 20.
- HERRE, A. W. C. T. AND G. S. MYERS. 1937. A contribution to the ichthyology of the Malay Peninsula. *Bull. Raffles Mus.* 13:5-75.
- HUBBS, C. L. 1944. Fin structure and relationships of the phallostethid fishes. *Copeia* 1944:69-79.
- HUBBS, C. L. AND L. C. HUBBS. 1945. Bilateral asymmetry and bilateral variation in fishes. *Pap. Mich. Acad. Sci. Arts Let.* 30:229-310.
- HUMPHRIES, C. J. AND L. R. PARENTI. 1986. *Cladistic biogeography*. Oxford Monographs on Biogeography No. 2. Clarendon Press, Oxford, England. 98 pp.

- IVANTSOFF, W., B. SAID, AND A. WILLIAMS. 1987. Systematic position of the family Dentatherinidae in relationship to Phallostethidae and Atherinidae. *Copeia* 1987:649-658.
- LADIGES, W., G. VON WAHLERT, AND E. MOHR. 1958. Die Typen und Typoide der Fische Sammlung des Hamburgischen Zoologischen Staatsinstituts und Zoologischen Museums. *Mitt. Hamburg Zool. Inst.* 56:155-167.
- LEVITON, A. E., R. H. GIBBS, JR., E. HEAL, AND C. E. DAWSON. 1985. Standards in herpetology and ichthyology: part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. *Copeia* 1985:802-832.
- MADDISON, W. P., M. J. DONOGHUE, AND D. R. MADDISON. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33:83-103.
- MANACOP, P. R. 1936. A new phallostethid fish with notes on its early development. *Philipp. J. Sci.* 59:375-381.
- MICKEVICH, M. F. 1978. Taxonomic congruence. *Syst. Zool.* 27:143-158.
- MYERS, G. S. 1928. The systematic position of the phallostethid fishes, with diagnosis of a new genus from Siam. *Am. Mus. Novit.* 295:1-12.
- . 1935. A new phallostethid fish from Palawan. *Proc. Biol. Soc. Wash.* 48:5-6.
- . 1937. Notes on phallostethid fishes. *Proc. U.S. Natl. Mus.* 84:137-143.
- NELSON, G. 1978. Ontogeny, phylogeny, paleontology, and the biogenetic law. *Syst. Zool.* 27:324-345.
- PARENTI, L. R. 1981. A phylogenetic and biogeographic analysis of cyprinodontiform fishes (Teleostei, Atherinomorpha). *Bull. Am. Mus. Nat. Hist.* 168:335-557.
- . 1984. On the relationships of phallostethid fishes (Atherinomorpha), with notes on the anatomy of *Phallostethus dunckeri* Regan, 1913. *Am. Mus. Novit.* 2779:1-12.
- . 1986a. Bilateral asymmetry in phallostethid fishes (Atherinomorpha), with description of a new species from Sarawak. *Proc. Calif. Acad. Sci.* 44:225-236.
- . 1986b. Homology of pelvic fin structures in female phallostethid fishes (Atherinomorpha, Phallostethidae). *Copeia* 1986:305-310.
- . 1986c. The phylogenetic significance of bone types in euteleost fishes. *Zool. J. Linn. Soc.* 87:37-51.
- PATTEN, J. M. AND W. IVANTSOFF. 1983. A new genus and species of atherinid fish, *Dentatherina merceri* from the western Pacific. *Japan. J. Ichthyol.* 29:329-339.
- PATTERSON, C. 1982. Morphological characters and homology. Pp. 21-74 in *Problems of phylogenetic reconstruction*. K. A. Joysey and A. E. Friday, eds. Academic Press, New York.
- REGAN, C. T. 1913. *Phallostethus dunckeri*, a remarkable new cyprinodont fish from Johore. *Ann. Mag. Nat. Hist.* 12:548-555.
- . 1916. The morphology of the cyprinodont fishes of the subfamily Phallostethinae, with descriptions of a new genus and two new species. *Proc. Lond. Zool. Soc.* 1916:1-26.
- ROBERTS, T. R. 1971a. The fishes of the Malaysian family Phallostethidae (Atheriniformes). *Breviora* 374:1-27.
- . 1971b. Osteology of the Malaysian phallostethid fish *Ceratostethus bicornis*, with a discussion of the evolution of remarkable structural novelties in its jaws and external genitalia. *Bull. Mus. Comp. Zool.* 142:393-418.
- ROSEN, D. E. 1964. The relationships and taxonomic position of the halfbeaks, killifishes, silversides, and their relatives. *Bull. Am. Mus. Nat. Hist.* 127:217-268.
- ROSEN, D. E. AND L. R. PARENTI. 1981. Relationships of *Oryzias*, and the groups of atherinomorph fishes. *Am. Mus. Novit.* 2719:1-25.
- SMITH, H. M. 1927. The fish *Neostethus* in Siam. *Science* 65:353-355.
- . 1929. Notes on some Siamese fishes. *J. Siam Soc. Nat. Hist., Suppl.* 8:11-14.
- . 1945. The fresh-water fishes of Siam, or Thailand. *Bull. U.S. Natl. Mus.* 188:1-622.
- SPRINGER, V. G. 1983. *Tyson belos*, new genus and species of western Pacific fish (Gobiidae, Xenisthmidae), with discussions of gobioid osteology and classification. *Smithson. Contrib. Zool.* 390:1-40.
- TAKITA, T. AND K. NAKAMURA. 1986. Embryonic development and prelarva of the atherinid fish, *Hypoatherina bleekeri*. *Japan. J. Ichthyol.* 33:57-61.
- TEWINKEL, L. E. 1939. The internal anatomy of two phallostethid fishes. *Biol. Bull.* 76:59-69.
- VILLADOLID, D. V. AND P. R. MANACOP. (1934) Issued 1935. The Philippine Phallostethidae, a description of a new species, and a report on the biology of *Gulaphallus mirabilis* Herre. *Philipp. J. Sci.* 55:193-220.
- WEBER, M. AND L. F. DEBEAUFORT. 1922. Phallostethidae. Pp. 381-383 in *The fishes of the Indo-Australian Archipelago IV*. Leiden, The Netherlands.
- WEITZMAN, S. H. AND S. V. FINK. 1985. Xenobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae). *Smithson. Contrib. Zool.* 421:1-121.
- WHITE, B. N., R. J. LAVENBERG, AND G. E. MCGOWEN. 1984. Atheriniformes: development and relationships. Pp. 355-362 in *Ontogeny and systematics of fishes*. H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr., and S. L. Richardson, eds. *Am. Soc. Ichthyol. Herp. Spec. Publ.* No. 1.
- WHITMORE, T. C., ED. 1987. Biogeographical evolution of the Malay Archipelago. Oxford Monographs on Biogeography No. 4. Clarendon Press, Oxford, England. 147 pp.
- WILEY, E. O. 1981. Phylogenetics; the theory and practice of phylogenetic systematics. John Wiley and Sons, New York. 439 pp.
- WINTERBOTTOM, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. *Proc. Acad. Nat. Sci. Philad.* 125:225-317.
- WOLTERECK, R. 1942a. Stufen der Ontogenese und der Evolution von Kopulationsorganen bei Neostethiden (Perceosoces, Teleostei). *Intl. Rev. Ges. Hydrobiol. Hydrogr.* 42:253-268.
- . 1942b. Neue Organe, durch postembryonale Umkonstruktion aus Fischflossen entstehend. *Intl. Rev. Ges. Hydrobiol. Hydrogr.* 42:317-355.